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**University of Alberta**

**Small-scale spatial patterns of boreal mixedwood forest vegetation**

**by**

**Steven W. Kembel**



A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment  
of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall, 2001





**University of Alberta**

**Faculty of Graduate Studies and Research**

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Small-scale spatial patterns of boreal mixedwood forest vegetation* submitted by Steven W. Kembel in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.





## ABSTRACT

In this study I examined the small-scale spatial structure of, and relationships between, boreal mixedwood canopy and understory vegetation. Seven 0.5 hectare study plots were established in mature and old boreal mixedwood forests in Alberta, Canada. Within each plot I mapped the location of all tree stems and sampled understory vegetation in 521 0.25-m<sup>2</sup> quadrats. Using spatial analysis techniques including Ripley's K analysis and wavelet analysis, I found that canopy and understory vegetation had very patchy spatial distributions at scales from 0.5 to 25 meters. The spatial arrangement of canopy trees appeared to influence spatial patterns of tree regeneration and understory plant community structure at a range of small spatial scales. Canopy conifers showed a stronger influence on the understory than canopy deciduous trees, and the overall influence of the canopy on the understory increased along a gradient of increasing conifer presence in the canopy.



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## CHAPTER 1

### GENERAL INTRODUCTION

#### Background

Studies of the spatial and temporal patterns in plant communities can lead to insights into the ecological processes which gave rise to those patterns. In forest communities, the spatial patterns of patches of canopy and understory vegetation often change as they establish, grow and die during the course of succession. Watt (1947) noted this in his classic paper on pattern and process in the plant community, pointing out that gaps in the canopy can influence the dynamics of vegetation patches in the understory. An understanding of the structure of, and relationships between, canopy and understory vegetation will be essential if we wish to understand and conserve biological diversity in forests which are increasingly affected by anthropogenic disturbance and management. In this thesis, I examine the spatial patterns of boreal mixedwood forest canopy and understory vegetation at small spatial scales.

The boreal mixedwood forests that cover much of Alberta are characterized by the presence of a mixture of shade-tolerant conifers and shade-intolerant deciduous trees in the canopy (Dix and Swan 1971, Rowe 1972, Corns and Annas 1986). After a stand-initiating disturbance such as fire, succession in these forests generally proceeds from initial dominance by shade-intolerant deciduous trees such as trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), towards increasing canopy dominance by shade-tolerant conifer trees such as white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*), which are able to regenerate under a closed canopy (Dix and Swan 1971, Bergeron 2000). In addition to changes in canopy composition and structure during boreal forest succession, the abundance and distribution of many understory plant species also change as stand age increases (Carleton and Maycock 1980, Morneau and Payette 1989, de Grandpré et al. 1993, Fortin et al. 1999).

A great deal of research has focused on the influence of forest tree canopies on the distribution of plants and resources in the understory, particularly with regards to the effects of canopy gaps on the understory (Platt and Strong 1989). Canopy gap research





has shown that the availability of many resources is different under gaps than under closed canopies (Collins et al. 1985, Vitousek and Denslow 1986, Canham et al. 1990, Kuuluvainen et al. 1993), and that small-scale spatial patterns of understory tree regeneration and plant community structure are often related to patterns of canopy structure (e.g. Kuuluvainen et al. 1993, Leemans 1991, Hubbell et al. 1999, Økland et al. 1999, Saetre 1999). In tropical and temperate forests, canopy gaps are important regeneration sites for many trees, and have been hypothesized to help maintain the high diversity of tree species found in these forests by allowing shade-intolerant species which cannot regenerate under a closed canopy to survive in a stand (Denslow 1987). A few studies examining the role of canopy gaps in boreal forests have found similar patterns of understory tree response to canopy gaps, with tree regeneration densities often being higher under canopy gaps than under closed canopies, especially in older forests (Leemans 1991, Liu and Hytteborn 1991, Kuuluvainen 1994, Kneeshaw and Bergeron 1998, Cumming et al. 2000).

Although the focus of most studies of canopy gaps has been the influence of canopy trees on understory trees, trees make up only a small part of the total species richness in many plant communities, and canopy trees can also influence the distribution of non-tree understory plant species (Schnitzer and Carson 2000). Understory plant cover, richness and diversity are often higher under canopy gaps (Beatty 1984, Collins et al. 1985, Dirzo et al. 1992, de Grandpré and Bergeron 1997, Goldblum 1997, Svenning 2000). Canopy structure, light availability, dispersal limitation, competition, herbivory, soil variables, site history and biogeographic processes can all affect the distribution of understory plant species at a range of spatial scales (Collins et al. 1985, Lieffers and Stadt 1994, Tonteri 1994, Dlott and Turkington 2000, Ehrlén and Eriksson 2000).

The patterns and processes which structure plant communities often change with the spatial scale of observation (Kotliar and Wiens 1990, Palmer 1990, Levin 1992, Jonsson and Moen 1998), and may vary between organisms which experience their environments at different spatial scales (Addicott et al. 1987, Wiens 1989). Despite our extensive knowledge of the stand- and landscape-level structure and composition of boreal mixedwood forests, there is very little information available regarding the small-scale structure of boreal mixedwood canopy and understory vegetation, or regarding the



small-scale spatial relationships between boreal mixedwood canopy trees, understory trees and understory vegetation.

## **Thesis Objectives**

The objectives of this thesis were (1) to quantify the small-scale spatial structure of, and relationships between, canopy and understory vegetation in mature and old boreal mixedwood forests; (2) to examine how canopy and understory species and species groups differed in their spatial structure and relationships; and (3) to examine how canopy and understory structure and relationships varied along a gradient of canopy composition and stand age, from younger broadleaved deciduous tree dominated stands, to older evergreen conifer tree dominated stands. In Chapter 2, I examine the spatial patterns of canopy and understory tree populations at a range of small spatial scales using point pattern analysis. In Chapter 3, I examine the structure of, and relationships between, canopy and understory vegetation using wavelet analysis and geostatistical techniques. In Chapter 4, I summarize my findings and discuss directions for future research related to this study.

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## CHAPTER 2

### SPATIAL PATTERNS OF BOREAL MIXEDWOOD TREE POPULATIONS

#### Introduction

Ecological patterns and processes can occur at many spatial scales, and numerous authors have addressed the importance of a multi-scale approach to ecological research (Palmer 1990, Levin 1992, Jonsson and Moen 1998). Phenomena such as disturbance, environmental heterogeneity, dispersal limitation and competition can all contribute to the spatial structure of forest tree populations at a range of spatial scales from individual plant neighbourhoods to landscapes. Although several studies have documented the spatial structure and relationships between canopy trees and understory trees in forests around the world (e.g. Mouer 1993, Szwagrzyk and Czerwczak 1993, Peterson and Squiers 1995, Busing 1998, Chen and Bradshaw 1999, Mast and Veblen 1999, Parish et al. 1999, Wells and Getis 1999, Plotkin et al. 2000), there is a lack of quantitative analysis of the spatial structure of boreal mixedwood tree populations.

The boreal mixedwood forests of western North America are characterized by the presence of both shade-tolerant evergreen coniferous species (e.g. white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*)) and shade-intolerant deciduous broadleaved species (e.g. trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*)) in the canopy (Dix and Swan 1971, Rowe 1972, Corns and Annas 1986). Many studies of boreal forests have documented the importance of large, stand-initiating disturbances such as fire in structuring these forests at the landscape and stand scale (Dix and Swan 1971, Heinzelman 1981). Typically, succession in these forests proceeds from initial dominance by shade-intolerant trees towards increasing dominance of the canopy by shade-tolerant species which are able to regenerate under a closed canopy (Dix and Swan 1971, Bergeron 2000).

Recent research has demonstrated that small-scale disturbances such as canopy gap creation can also play a very important role in structuring boreal forests (Leemans 1991, Liu and Hytteborn 1991, Kuuluvainen 1994, Kneeshaw and Bergeron 1998,





Cumming et al. 2000), especially in older forests where gaps created by canopy mortality due to windthrow, insect outbreaks or disease can be important tree regeneration sites (Kuuluvainen 1994). Light levels, temperature, and soil nutrient and moisture availability are often higher under canopy gaps than under closed canopies (Vitousek and Denslow 1986, Denslow 1987), although at boreal latitudes, the oblique angle of incident radiation may prevent direct radiation from reaching the forest floor in gaps below a certain size threshold (Canham et al. 1990). Boreal forest canopy gap area increases with stand age, and in old stands, which escape large-scale disturbance for extended periods of time, shade-intolerant tree species that would otherwise be unable to survive in a stand may be able to regenerate in canopy gaps (Kneeshaw and Bergeron 1998).

Numerous studies have investigated forest structure and canopy gap dynamics from a spatial analysis perspective (Dale 1999), which allows ecological patterns and relationships to be studied at several spatial scales simultaneously. Generally, these studies have found that canopy trees tend to be overdispersed from one another at small spatial scales, with competition for resources with neighbouring trees leading to the death of competitively inferior trees and a more regular spatial pattern with increasing stand age (Peet and Christensen 1987, Kenkel 1988, Moeur 1993, but see Peterson and Squiers 1995). Canopy trees are usually either randomly arranged or clumped at larger spatial scales, due to spatially random post-disturbance tree establishment (Kenkel 1988) or environmental heterogeneity causing variation in establishment, growth and mortality (Szwagrzyk and Czerwczak 1993, Chen and Bradshaw 1999). Understory trees are generally strongly clumped in their spatial distribution, due to patchy distributions of propagules and germination substrates, and the effects of canopy structure, soil resources and herbivory leading to patchy establishment and survival (Leemans 1991, Larsen and Bliss 1998, Chen and Bradshaw 1999, Clark et al. 1999, Hubbell et al. 1999). Canopy and understory trees are often spatially segregated from each other at small spatial scales when regeneration occurs primarily in canopy gaps (Leemans 1991, Moeur 1993, Chen and Bradshaw 1999). Although a few studies have examined the spatial structure of boreal tree populations (Kenkel 1988, Leemans 1991, Kuuluvainen et al. 1998), the majority have been carried out in other forest types such as tropical forests, temperate forests, and cordilleran forests.



The objectives of this study were to quantify the spatial patterns of boreal mixedwood tree populations at a range of spatial scales, and to determine if the arrangement of canopy trees influences the distribution of understory trees in mature and old boreal mixedwood forests. I was also interested in determining if canopy-understory spatial relationships varied between tree species, or between stands dominated by shade-tolerant versus shade-intolerant canopy trees.

I hypothesized that canopy-understory spatial relationships should be stronger in conifer-dominated stands, due to the ability of canopy conifers to reduce light levels in the understory below levels found under deciduous trees (Canham et al. 1994, Lieffers and Stadt 1994, Constabel and Lieffers 1996, Messier et al. 1998) and thus to influence understory tree distribution patterns. I also hypothesized that shade-intolerant understory trees should show a stronger relationship with canopy tree distributions than shade-tolerant understory trees, because shade-intolerant trees should be more dependent on the light available in canopy gaps for establishment and survival (Whitmore 1989).

## **Methods**

### ***Study sites***

During the summer of 1999, I established seven study plots at the Ecosystem Management by Emulating Natural Disturbance (EMEND) experimental site located northwest of Peace River, Alberta. The forests at this site in the Dry Boreal Mixedwood natural subregion of the province (Achuff 1992) are predominantly boreal mixedwood forest stands. Each study plot was a square measuring either 100 meters on a side (one plot) or 70 meters on a side (six plots). All plots were located in “control” compartments of the EMEND experiment, which had not been recently logged or burned. Each plot was situated randomly within a control compartment, with the restriction that it be at least 50 meters from forest edges, contain no major topographical features, have a slope of 1% or less, and not contain signs of major human disturbance such as trails or experimental manipulations of vegetation. Table 2.1 contains a summary of the characteristics of the seven study plots established at the EMEND site.



## *Data collection*

Each study plot consisted of a 50 x 50 meter core area surrounded on each side by a buffer of either 25 meters (plot C1) or 10 meters (all other plots). Field layout of the plot was accomplished with the use of a Pentax theodolite to ensure accurate measurement of corner locations. All plots were oriented such that the north-south axis of the plot was parallel to a bearing of 0 degrees (true north). The outer corners of each plot were permanently marked with metal stakes to allow future revisitation of the plots. In each plot, the location of every live tree stem taller than 2 meters was mapped using the theodolite. I placed the theodolite at each of the corners of the plot while an assistant moved to each tree stem in the plot with a measuring prism and recorded tree species identity and diameter at breast height (DBH). Each tree was marked with paint once it had been mapped to ensure all trees were measured and to prevent the mapping of a particular stem more than once. I measured the angle and distance to the tree, and measured the angle to treetop, live crown and tree base for each stem using a clinometer. This allowed mapping of the location, height and height to live crown of each stem once measurements were converted from angles and distances to (x,y) coordinates and heights within the plot. Coordinates of trees in each plot were expressed as eastings (x) and northings (y) in meters from the southwest corner of the plot.

Within the 50 x 50 meter core area, I also mapped the location of all live trees less than 2 meters height. The core area was divided into 5 meter grid cells and the location and height of all living tree stems less than 2 meters tall were recorded in each cell using measuring tapes and 3-way prisms to ensure accuracy.

After examination of the raw data, it became apparent that the use of a clinometer to measure tree height and height to live crown was an imprecise method. For trees located less than 5-10 meters away from the mapping station, it was difficult to measure the angle to treetop and live crown, and small errors in measurement were magnified when converting from measured angles to heights at small distances. For this reason, published models of the relationship between DBH and tree height for Alberta tree





species (Huang et al. 1992) were used to obtain height measurements for all trees taller than 2 meters.

### *Data analysis*

All tree spatial patterns were analyzed using Ripley's K function (Ripley 1977), a method frequently applied to the analysis of spatial point patterns (Andersen 1992, Penttinen et al. 1992, Haase 1995). Ripley's K function allows the statistical measurement of the degree of clumping or overdispersion of a spatial point pattern at a range of spatial scales. The function is calculated using the formula (Ripley 1977):

$$\hat{K}(t) = A \sum_i^n \sum_j^n w_{ij} I_t(i, j) / n^2 \quad (2.1)$$

This formula involves the counting of the number of points  $j$  within a radius  $t$  of each point  $i$  in the plot.  $A$  is the plot area,  $n$  is the number of points,  $w_{ij}$  is a weight applied to correct for edge effects (Haase 1995) and  $I_t(i, j)$  is a function which equals 1 for points within radius  $t$  of the focal point, and 0 otherwise. I converted  $\hat{K}(t)$  to the function  $\hat{L}(t)$  (Diggle 1983):

$$\hat{L}(t) = \sqrt{\hat{K}(t) / \pi} - t \quad (2.2)$$

This transformation standardizes the statistic such that spatially random patterns generated using a Poisson process have an expected  $\hat{L}(t)$  of zero, with positive  $\hat{L}(t)$  indicating clumping and negative  $\hat{L}(t)$  indicating overdispersion. I calculated  $\hat{L}(t)$  for spatial scales from 0 to 25 meters, and created 95% confidence intervals based on 100 randomizations of the point pattern.  $\hat{L}(t)$  values outside the bounds of the confidence intervals at a given scale indicate a spatial pattern that differs significantly from that expected from a completely random Poisson process.



A bivariate version of the function was used to interpret spatial associations between different groups of trees. The  $\hat{K}_{1,2}(t)$  function is calculated for two groups of points using the formula (Diggle 1983):

$$\hat{K}_{1,2}(t) = A \sum_i^{n_1} \sum_j^{n_2} w_{ij} I_t(i, j) / n_1 n_2 \quad (2.3)$$

The variables in the bivariate formula are the same as those used in the univariate form, with  $n_1$  and  $n_2$  being the number of points in each group. The bivariate function can also be expressed as the standardized statistic (Upton and Fingleton 1985):

$$\hat{L}(t) = \sqrt{[n_2 \hat{K}_{1,2}(t) + n_1 \hat{K}_{2,1}(t)] / \pi(n_1 + n_2) - t} \quad (2.4)$$

The expected value of the bivariate  $\hat{L}(t)$  is zero for two groups which show no spatial association at a given scale, positive for aggregated patterns and negative for segregated patterns. Using 100 randomizations of each group's stem locations, 95% confidence intervals for the bivariate  $\hat{L}(t)$  statistic were obtained in the same manner as the univariate case.

In each plot, canopy and understory tree patterns were analyzed separately. Based on tree height frequency distributions (Figure 2.1), I defined canopy trees as all trees taller than 10 meters, and understory trees were defined as all trees shorter than 10 meters, except in plot M1, where the canopy/understory cutoff was set at 5 meters. Canopy trees were further divided into conifer and deciduous species groups for analysis, and understory trees were analyzed separately by species. In each plot, I calculated Ripley's K function using tree stem locations of all canopy tree groups and understory species which had at least 20 stems in the core area of that plot (Table 2.2). Ripley's bivariate K analysis was also performed for all pairwise combinations of canopy tree groups present in each plot (all trees, conifer trees, deciduous trees) versus each understory tree species with at least 20 stems in that plot.



## Results

Trembling aspen and white spruce were the dominant canopy and understory species in all study plots, although smaller numbers of balsam fir, balsam poplar and white birch were found in some plots (Table 2.2). Although there were white spruce trees present in all height classes (Figure 2.1), there were no trembling aspen trees between 5 and 15 meters tall in any of the plots, suggesting that understory trembling aspen trees were failing to reach the canopy in these stands.

Spatial patterns of canopy trees were variable among plots (Figure 2.2, Figures 2.7-2.10), with most plots showing either random or overdispersed spatial patterns at small scales (<5 meters), and random or clumped spatial patterns at larger spatial scales (>5 meters). In plots where both conifer and deciduous trees were present in the canopy, these two canopy tree groups were often segregated at a range of spatial scales (Figure 2.3).

All species of understory trees were significantly clumped in six of the seven plots. Significant clumping occurred at scales from 2 to 25 meters, although most species showed the strongest clumping at scales between 5 and 15 meters (Figure 2.4).

Canopy - understory spatial relationships were highly variable, but a general trend was that understory trees of all species tended to be random or segregated from canopy trees at small scales (<5 meters), and random or aggregated with canopy trees at larger spatial scales (>5 meters). There were several exceptions to this trend, and the nature and strength of canopy-understory spatial relationships varied between canopy tree types, understory tree species and stand type.

Understory white spruce trees were significantly segregated from all canopy trees at small spatial scales in four of the six plots in which they were present (Figure 2.5), and tended to be either aggregated or randomly arranged with respect to canopy trees at larger spatial scales. Exceptions to this trend were found in plots M2 and C3, where understory white spruce were significantly aggregated with canopy trees at small spatial scales.

Understory aspen trees were segregated from all canopy trees at small spatial scales in both Aspen-dominated plots (A1 and A2), but were variously aggregated,





random or segregated at small scales with respect to all canopy trees in the Conifer-dominated and Mixed plots in which they were present (Figure 2.6).

Sufficient numbers of understory balsam poplar and white birch for analysis were found in several plots (A1, A2, C3). Understory trees of these species were segregated from canopy trees at small to intermediate spatial scales. In plot M1, a large number of understory balsam fir trees were present, and these trees were strongly aggregated with canopy trees at scales less than 10 meters.

Understory trees showed different spatial relationships with canopy conifers versus canopy deciduous trees in several plots, and their spatial relationships sometimes varied between plots. In several Conifer-dominated and Mixed plots, understory white spruce trees were segregated from canopy conifer trees, but aggregated with canopy deciduous trees at larger spatial scales (Figure 2.5). Understory aspen tended to be aggregated with canopy conifers in Conifer-dominated and Mixed plots, but were segregated from canopy conifers in Aspen-dominated plots, segregated from canopy deciduous trees at small scales in all plots, and often aggregated with deciduous canopy trees at larger scales (Figure 2.6).

## Discussion

The spatial patterns of boreal mixedwood tree species observed in this study were consistent with those found in other studies of forest spatial structure. Canopy trees were frequently overdispersed at small spatial scales, a pattern often explained as the result of competition with neighbouring trees leading to tree mortality and an increasingly regular distribution of stems in older stands (Kenkel 1988). Understory trees were strongly clumped at all spatial scales, a probable result of clumped seed dispersal, patchy regeneration microsite availability and the influence of canopy gaps (Leemans 1991, Chen and Bradshaw 1999, Mast and Veblen 1999, Parish et al. 1999). The patterns I observed confirmed that a multi-scale approach to describing forest structure is very useful, since the ecological patterns and relationships I observed often changed with the spatial scale of investigation. Significantly non-random spatial patterns and associations were found at all spatial scales examined, from 0 to 25 meters.



Although canopy gaps appeared to be important as regeneration sites for both white spruce and trembling aspen, these two species showed differences in the way they responded to canopy tree spatial patterns. White spruce is a shade-tolerant species which reproduces from seed (Burns and Honkala 1990). Although white spruce seedlings are able to survive under a closed canopy (Lieffers et al. 1996), seedling survival and growth are higher in canopy gaps due to the increased availability of resources such as light (Kuuluvainen et al. 1993, Pukkala et al. 1993). White spruce seedling and sapling densities were highest in canopy gaps in the study plots, and the continuous distribution of white spruce tree heights (Figure 2.1) suggested that some of these understory trees were reaching the canopy.

In mature boreal forests, trembling aspen regeneration occurs primarily via suckering of the root systems of clonal trees (Peterson and Peterson 1990). The increased light availability and soil temperatures in large canopy gaps may lead to increased trembling aspen density in these gaps (Kneeshaw and Bergeron 1998, Cumming et al. 2000), although due to the oblique angle of incident radiation at boreal latitudes, light levels in small gaps may not be greatly increased relative to those in surrounding closed canopy areas (Canham et al. 1990, Ban et al. 1998). Herbivory by ungulates is also a major source of mortality in understory trembling aspen, which can prevent understory trees from surviving to reach the canopy (Cumming et al. 2000). Understory trembling aspen trees did not show clear spatial patterns of occurring in canopy gaps in most of the plots in this study, and in a few plots actually showed higher densities under conifer canopies (Figure 2.4, Figures 2.6-2.9). Total gap area and gap sizes in the seven study plots may not have been sufficiently large to allow increased establishment and survival of understory trembling aspen in gaps, because no trembling aspen trees were found to be recruiting into the canopy (Figure 2.1). The clonal nature of aspen trees may have allowed the production and temporary survival of suckerlings under a closed canopy, through the allocation of resources to suckerlings from existing root systems (Peterson and Peterson 1990).

Gaps were less important as sites for tree regeneration in Aspen-dominated plots. This may have been caused by the greater dichotomy in environmental conditions between gap and non-gap microsites in Conifer-dominated and Mixed plots, perhaps due



to the ability of conifer canopy trees to reduce understory light levels below thresholds needed for seedling growth or survival (Lieffers and Stadt 1994, Messier et al. 1998). Differences in leaf and crown structure and composition between shade-intolerant and shade-tolerant trees results in the higher light extinction coefficients of shade-tolerant species such as white spruce (Canham et al. 1994). Light levels under closed hardwood canopies may be as high as 40% of ambient, while under a closed conifer canopy light levels may be reduced to less than 5% of ambient (Lieffers and Stadt 1994). The result of this is that shade-tolerant species such as white spruce are able to establish and survive under closed aspen and poplar canopies, but rarely so under dense white spruce and balsam fir canopies.

The segregation of understory white spruce from canopy trees in Conifer-dominated and Mixed plots indicated that white spruce regeneration densities were often extremely high under gaps versus under closed canopies in these plots. While white spruce densities were higher in canopy gaps in the Aspen-dominated plots, regenerating white spruce were also found under the closed aspen canopy in these stands. In some of the Conifer-dominated plots, white spruce densities were relatively high under canopy aspen trees (Figure 2.7), indicating that the regenerating white spruce seedlings may be able to respond to the increased light availability under canopy aspen trees in the same way that they respond to canopy gaps.

This study did not address the mechanisms of canopy influence on understory trees. The high variability of spatial patterns and relationships in this study were likely a result of the influence of variables which could not be addressed using the spatial point pattern approach to studying forest structure. The greater influence of canopy conifers on understory tree distributions may be due to other interspecific differences in addition to their higher light extinction abilities, such as belowground competitive ability or tree effects on soil nutrient and moisture conditions (Pelletier et al. 1999). While canopy effects on light availability are generally thought to be the primary influence on tree regeneration patterns in boreal forests (Lieffers et al. 1999), belowground competition from canopy trees may also play an important role, although aboveground canopy gaps are sometimes belowground root biomass gaps (Wilczynski and Pickett 1993, but see





Campbell et al. 1998). Few studies have been able to differentiate between the effects of above- and below-ground tree competition in forest ecosystems (Riegel et al. 1995).

Microsite conditions such as moisture and nutrient availability or availability of suitable germination substrates can interact with light availability to determine tree regeneration success (Kuuluvainen et al. 1993). Several studies have demonstrated that environmental conditions in canopy gaps vary with stand age, gap age and gap size (de Grandpré and Bergeron 1997, Kneeshaw and Bergeron 1998), which can influence tree regeneration success in gaps. Competition for light and soil resources from understory vegetation (Hogg and Lieffers 1991, Lieffers and Stadt 1994, Messier et al. 1998) and dispersal limitation (Clark et al. 1999, Hubbell et al. 1999) can also prevent trees from establishing successfully in gaps.

## Conclusions

This study has illustrated that the spatial patterns of boreal mixedwood tree populations are similar to those of trees in other forest types. Both canopy and understory trees were distributed in a spatially non-random fashion at several spatial scales in most plots. Spatial analyses illustrated the importance of canopy structure at several spatial scales in determining distribution patterns of understory trees in mature and old boreal mixedwood forests.

The hypothesis that canopy-understory spatial relationships would be stronger in Conifer-dominated and Mixed stands was supported. Canopy conifer trees had a greater influence on the spatial distribution of understory trees, both in terms of the larger number of significant spatial relationships between conifers and understory trees, and in terms of the larger magnitude of those significant relationships that were present. In some Conifer-dominated and Mixed stands, understory trees densities were nearly as high under Aspen trees as under actual canopy gaps. Light levels in Aspen-dominated stands may have been high enough to allow regeneration of shade-tolerant white spruce seedlings throughout the stand.

The hypothesis that shade-intolerant species such as aspen would be more dependent on canopy gaps as regeneration sites was not supported. Shade-tolerant white



spruce densities were much higher under canopy gaps than under closed canopies, while shade-intolerant Aspen suckerlings were often only slightly more common in gaps and were generally found throughout all study plots at a low density. Factors such as herbivory, dispersal limitation and light and soil temperature increases insufficient to trigger suckering in the small canopy gaps in the study plots, may all be contributing to the failure of understory Aspen to reach the canopy.

Further studies which examine a broader range of post-disturbance stand ages, and which examine individual study plots in more detail by aging trees or experimentally manipulating canopy structure, will be needed to link observed spatial patterns to the ecological processes which structure boreal mixedwood forests at multiple spatial scales.



Table 2.1. Attributes of seven study plots located at the EMEND experiment in Alberta, Canada.

Plot	EMEND Canopy Type Classification	EMEND Compartment	Mean Canopy Tree Age (years)	Plot core area tree basal area (m <sup>2</sup> /ha)			Plot core area tree density (stems/ha)				
				Conifer	Deciduous	Total	Canopy		Understory		Total
							Conifer	Deciduous	Conifer	Deciduous	
A1	Aspen	856	90	0.2	8.0	8.1	4	492	552	3056	4104
A2	Aspen	948	80	0.5	7.5	8.0	72	736	244	2820	3872
M1	Mixed	904	130	9.2	2.9	12.1	564	180	1324	292	2360
M2	Mixed	937	120	9.9	2.5	12.3	668	112	168	1580	2528
C1	Conifer	918	120	9.4	2.5	11.9	868	156	1072	1324	3420
C2	Conifer	930	130	10.6	1.0	11.7	660	56	164	1532	2412
C3	Conifer	889	130	8.1	0.0	8.1	572	0	188	300	1060

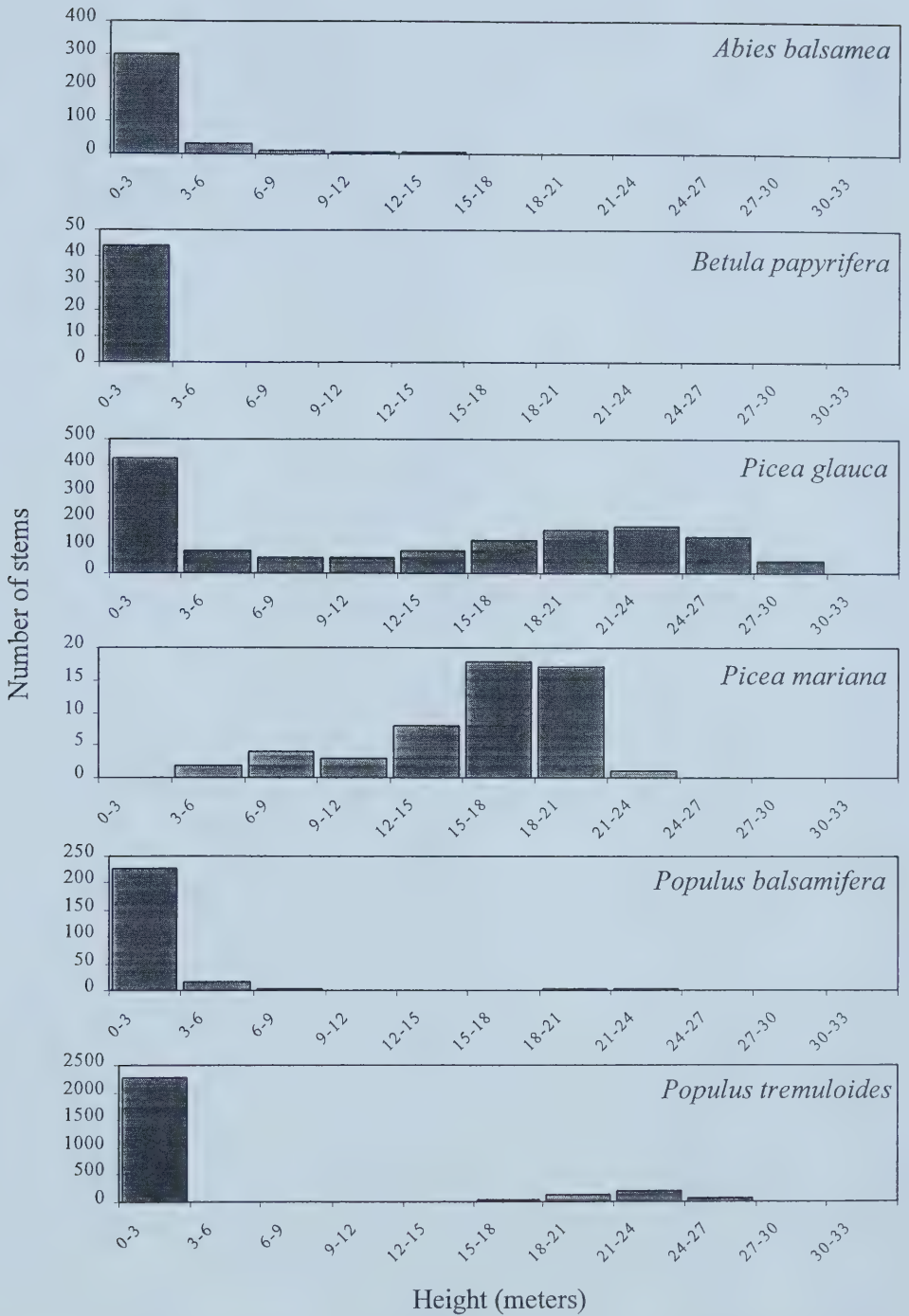




**Table 2.2.** Stem counts by species for canopy and understory trees in the core area of seven study plots located at the EMEND experiment in Alberta, Canada.

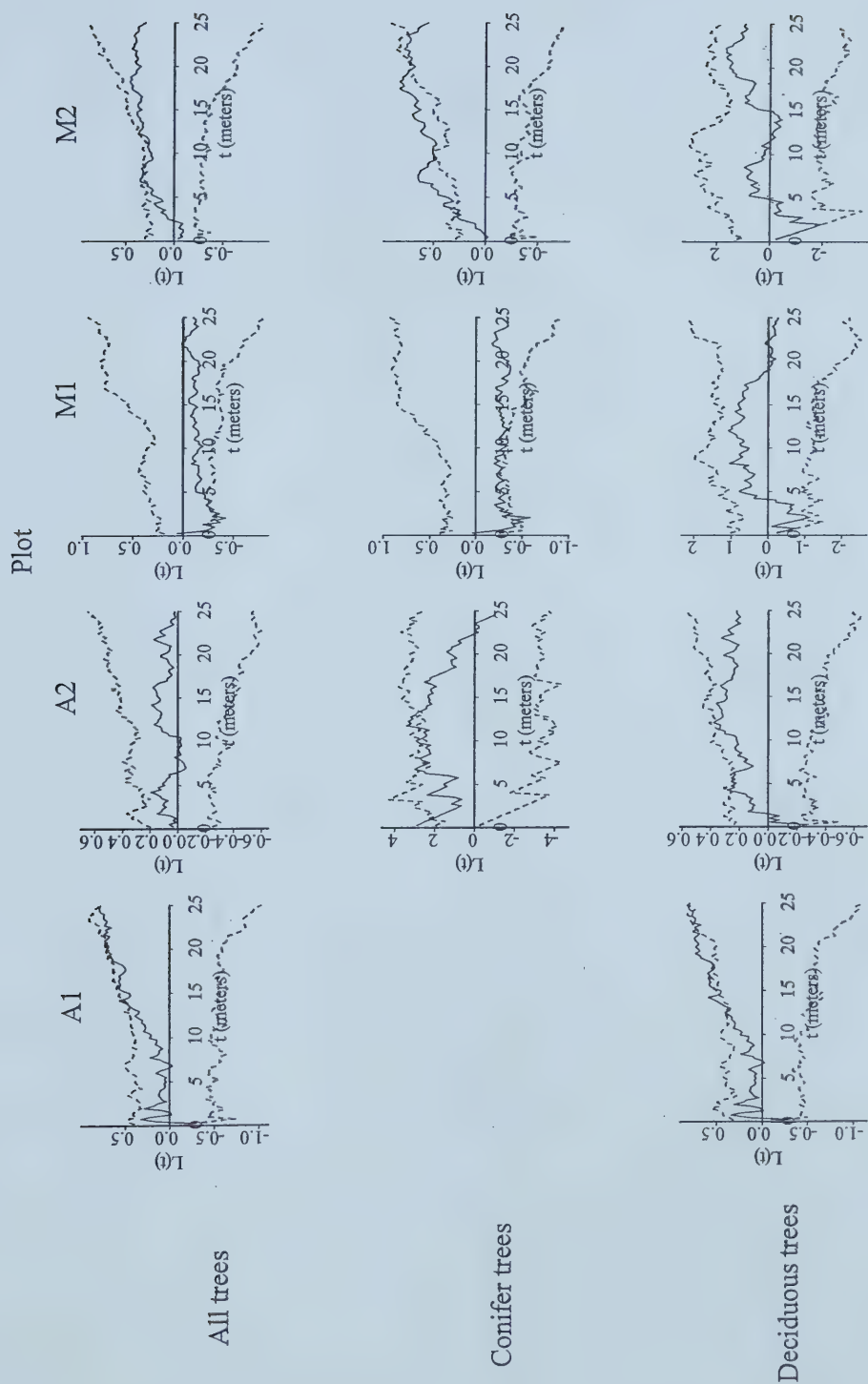
Stratum	Species		Core area stem count								
	Common name	Scientific name	A1	A2	M1	M2	C1	C2	C3		
Canopy	Balsam fir	<i>Abies balsamea</i>			20						
	White birch	<i>Betula papyrifera</i>			1						
	White spruce	<i>Picea glauca</i>	1	18	120	167	216	164	98		
	Black spruce	<i>Picea mariana</i>						1	45		
	Lodgepole pine	<i>Pinus contorta</i>			1		1				
	Balsam poplar	<i>Populus balsamifera</i>	6				2				
	Trembling aspen	<i>Populus tremuloides</i>	117	184	44	28	37	14			
Understory	Balsam fir	<i>Abies balsamea</i>	7	1	323			1	1		
	White birch	<i>Betula papyrifera</i>	21	1		2	8		15		
	White spruce	<i>Picea glauca</i>	131	60	8	42	265	40	38		
	Black spruce	<i>Picea mariana</i>							8		
	Lodgepole pine	<i>Pinus contorta</i>					2				
	Balsam poplar	<i>Populus balsamifera</i>	182	67							
	Trembling aspen	<i>Populus tremuloides</i>	521	601	68	393	322	383			
Total			986	932	585	632	854	603	205		





**Figure 2.1.** Height distributions for tree species totaled over seven study plots located at the EMEND experiment in Alberta, Canada.

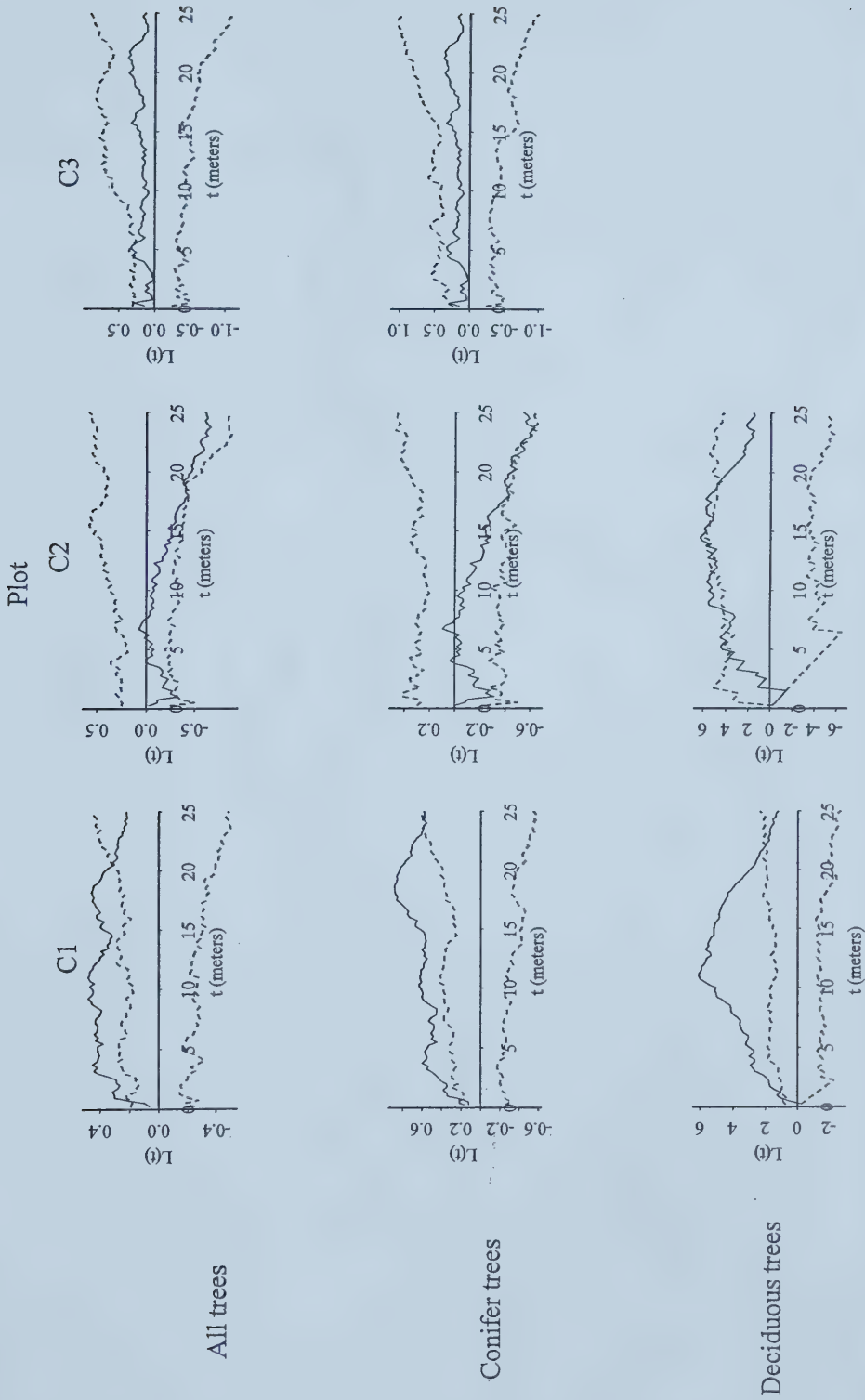




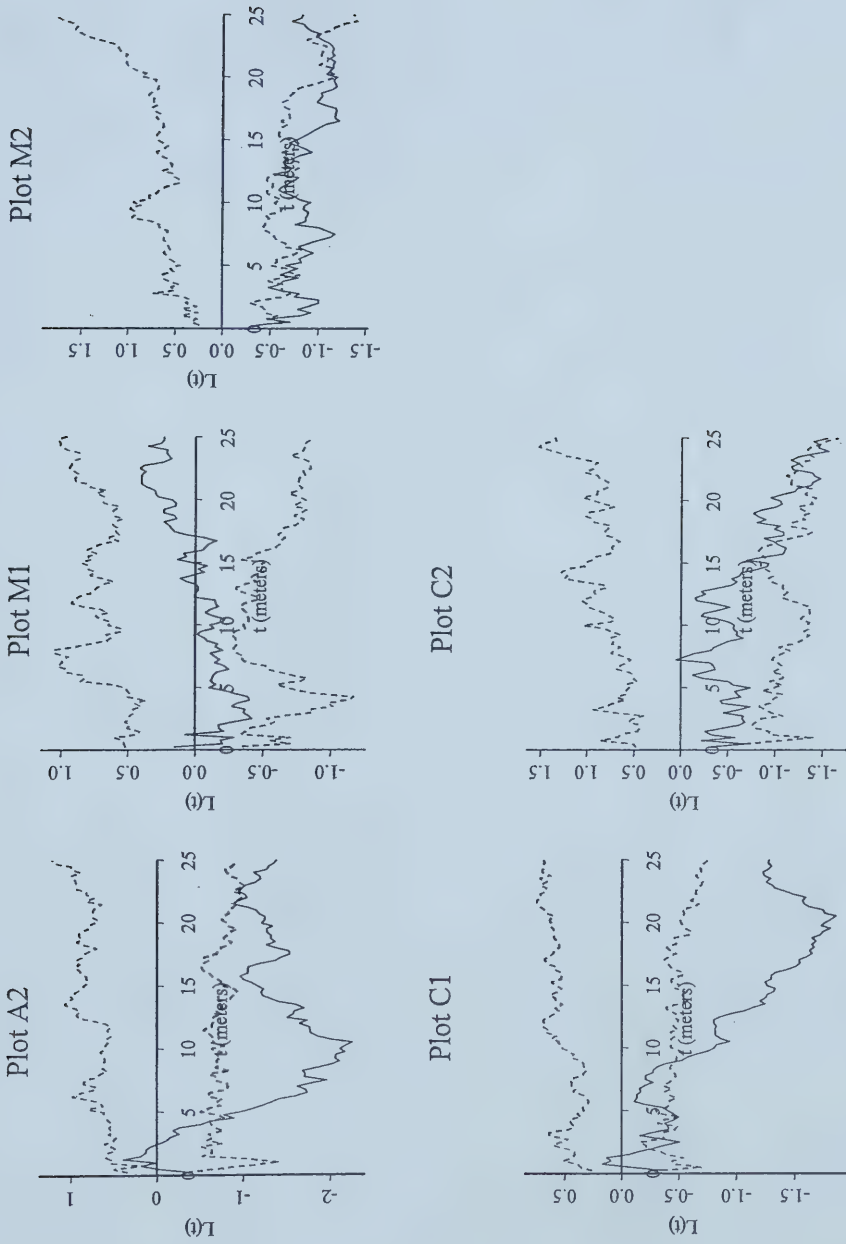
**Figure 2.2.** Plot of Ripley's univariate K results ( $\hat{L}(t)$ ) versus scale ( $t$ ) for canopy tree groups (all trees, conifer trees, deciduous trees) in all study plots in which a group had at least 20 canopy tree stems present. Solid lines are  $\hat{L}(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate clumping, negative scores indicate overdispersion.





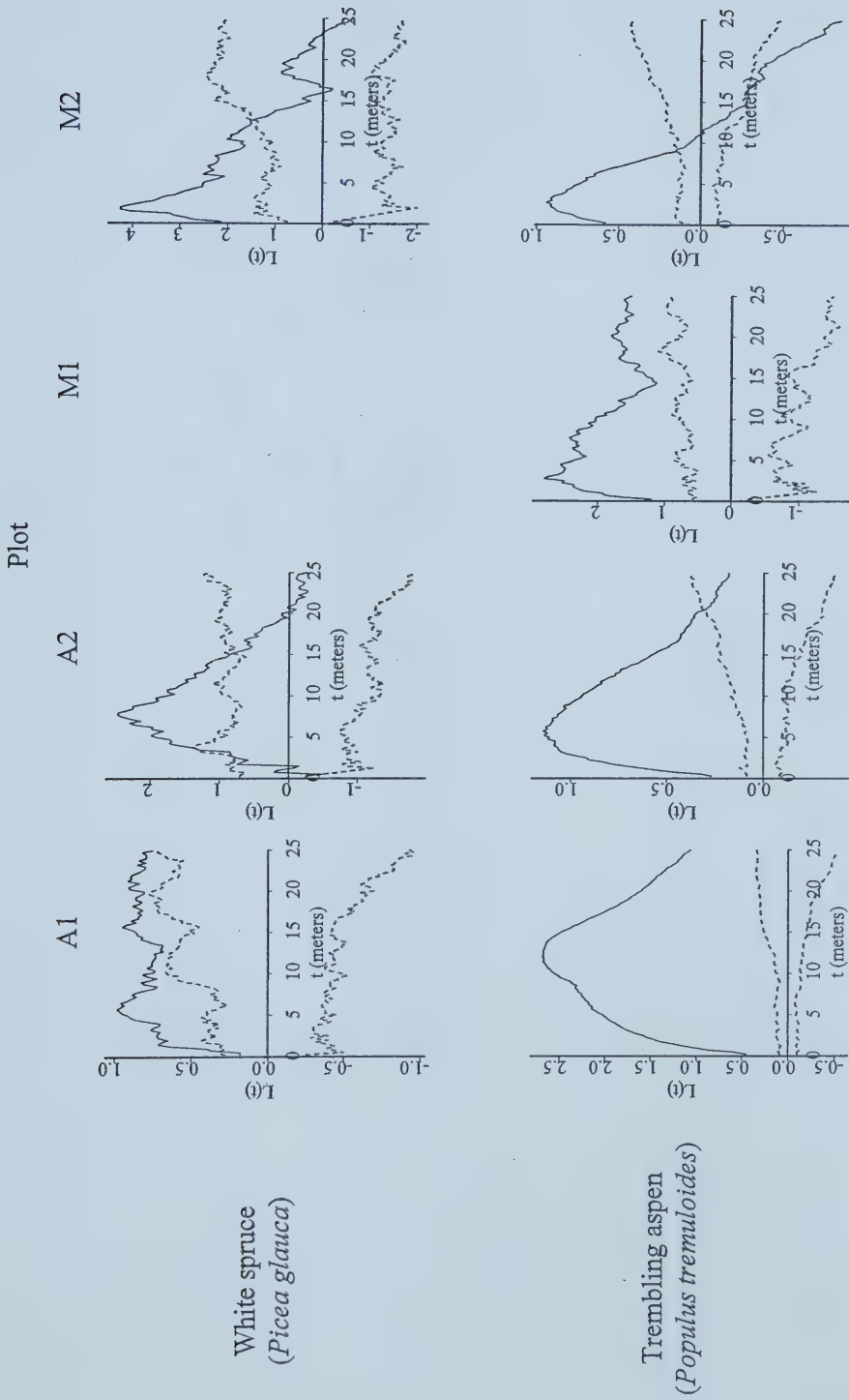






**Figure 2.3.** Plot of Ripley's bivariate K results ( $\hat{L}(t)$ ) versus scale ( $t$ ) for conifer canopy trees versus deciduous canopy trees in all study plots in which both groups had at least 20 canopy tree stems present. Solid lines are  $\hat{L}(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate clumping, negative scores indicate overdispersion.

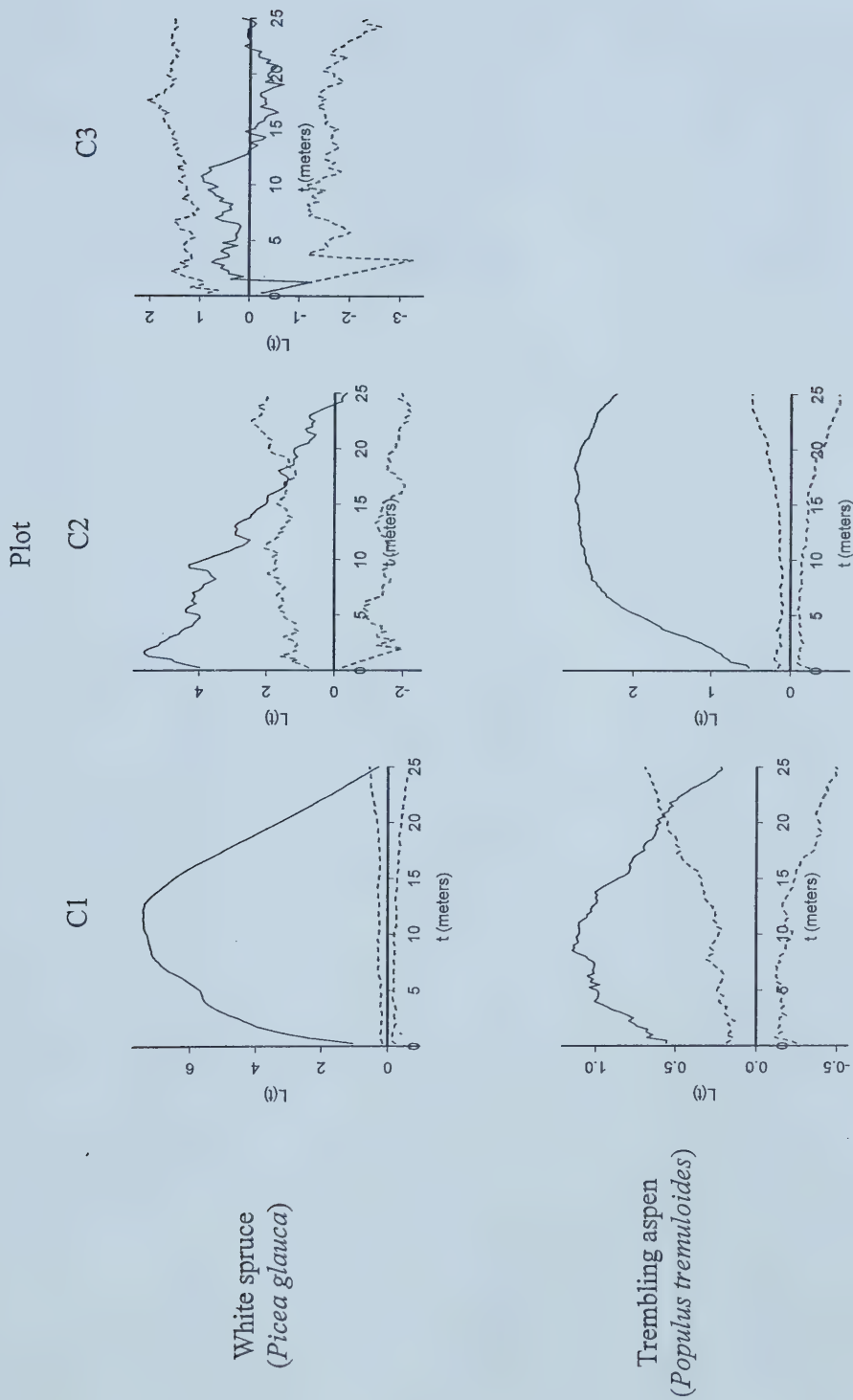




**Figure 2.4.** Plot of Ripley's univariate K results ( $\hat{L}(t)$ ) versus scale ( $t$ ) for understory white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) trees in all study plots in which a species had at least 20 tree stems present. Solid lines are  $\hat{L}(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate clumping, negative scores indicate overdispersion.

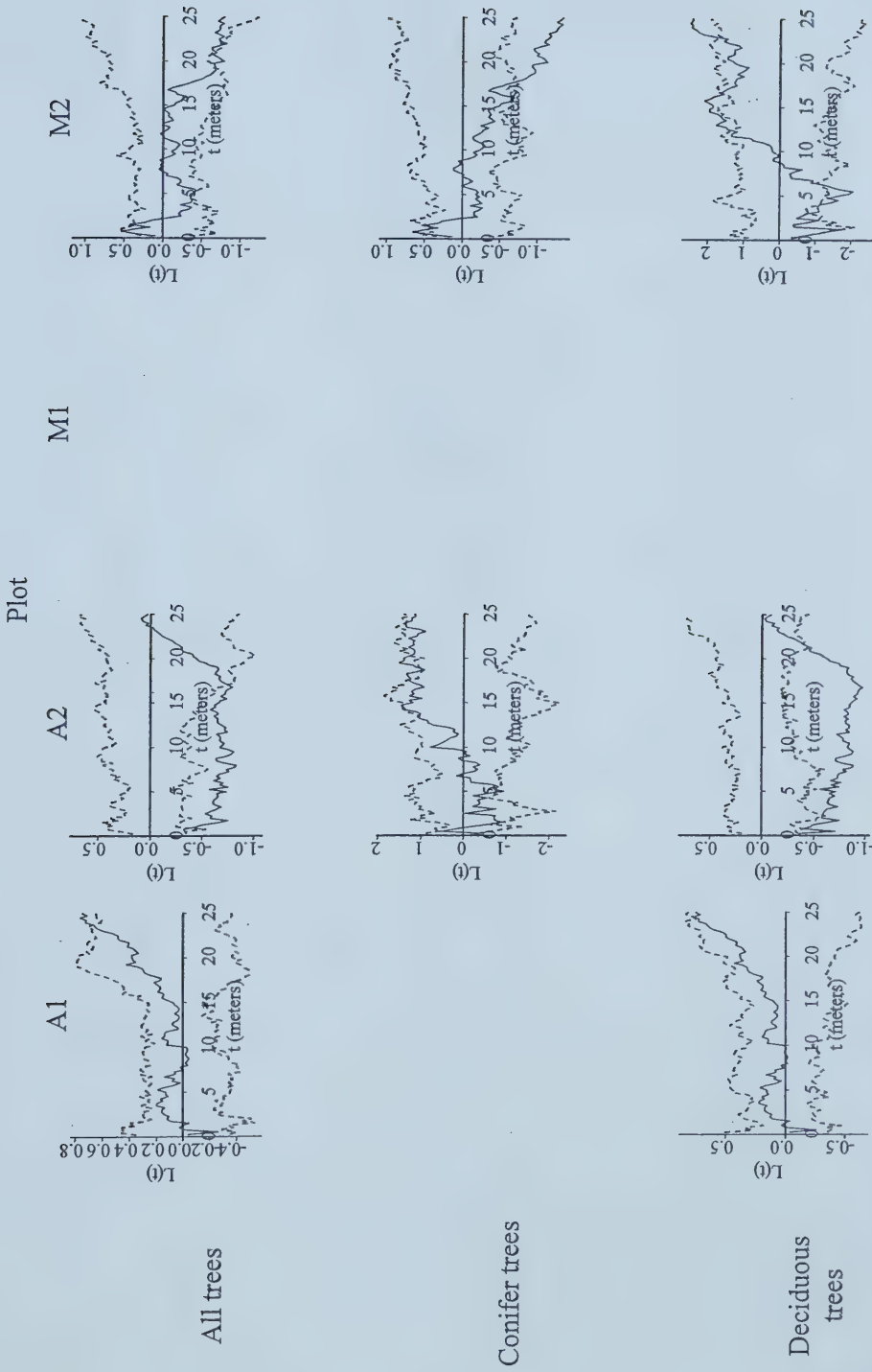






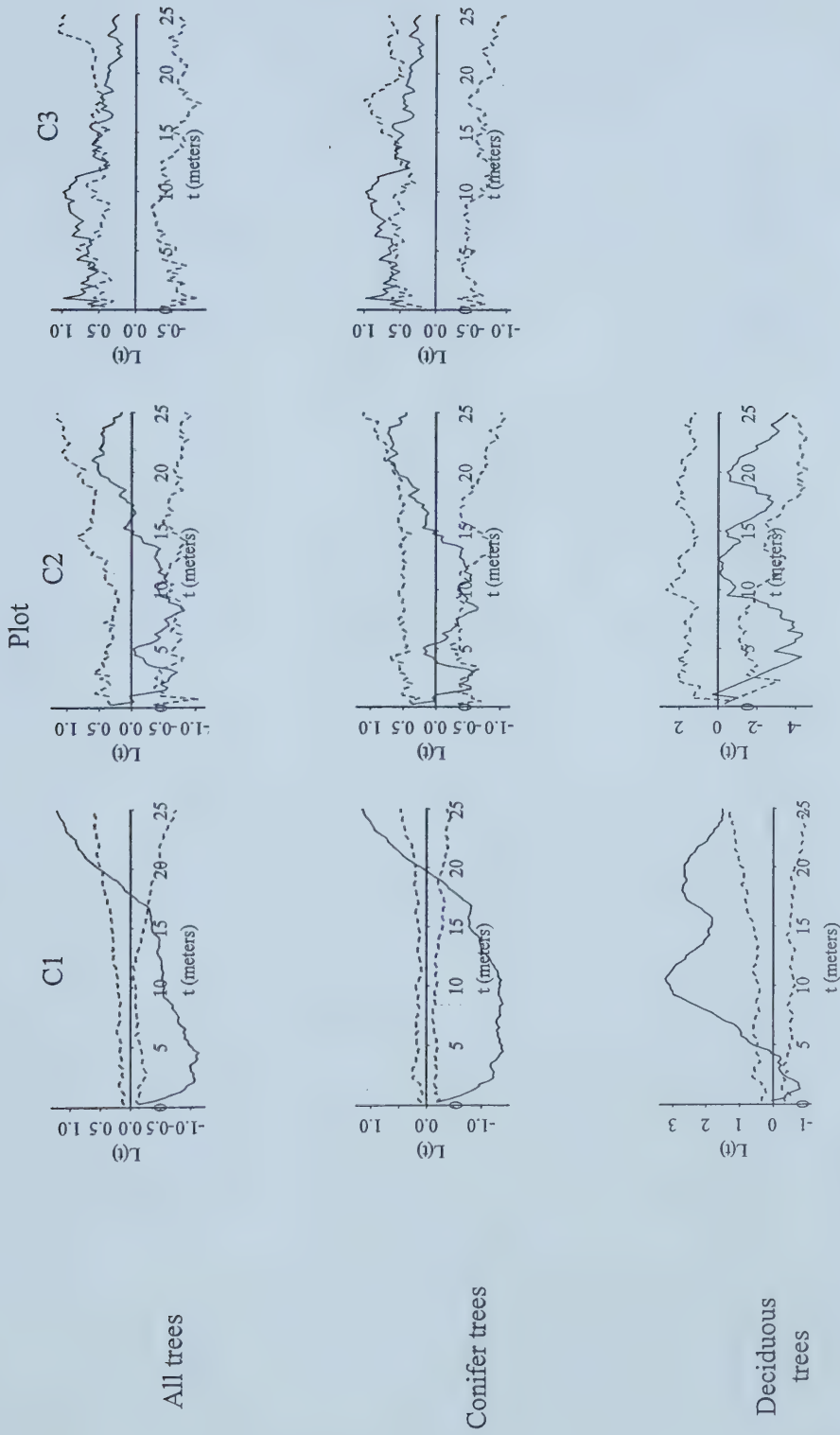
**Figure 2.4 continued.** Plot of Ripley's univariate K results ( $\hat{L}(t)$ ) versus scale ( $t$ ) for understory white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) trees in all study plots in which a species had at least 20 tree stems present. Solid lines are  $\hat{L}(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate clumping, negative scores indicate overdispersion.





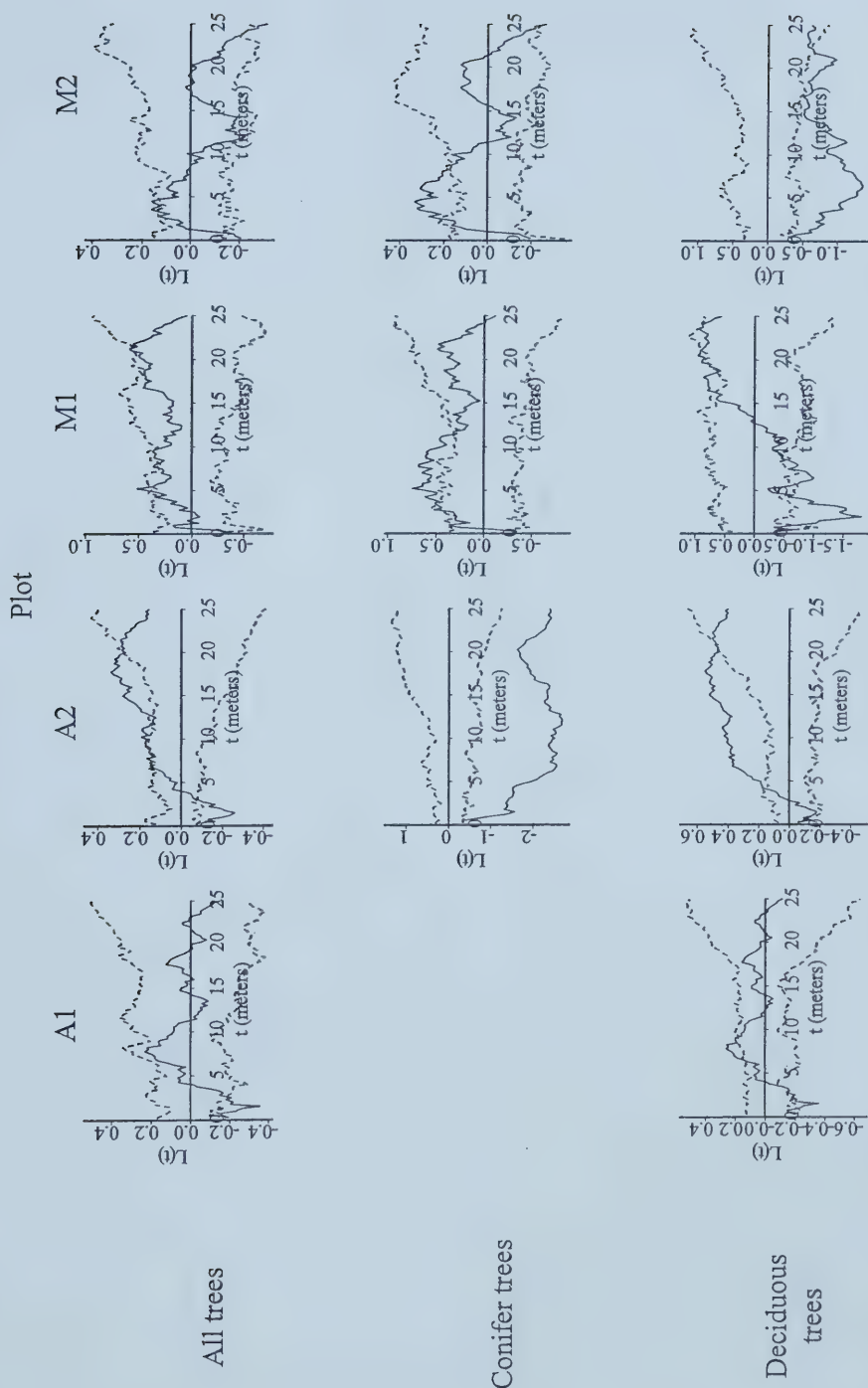
**Figure 2.5.** Plot of Ripley's bivariate K results ( $L(t)$ ) versus scale ( $t$ ) for canopy tree groups (all trees, conifer trees, deciduous trees) versus understory white spruce (*Picea glauca*) trees in all study plots in which both groups had at least 20 tree stems present. Solid lines are  $L(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate aggregation, negative scores indicate segregation.





**Figure 2.5 continued.** Plot of Ripley's bivariate K results ( $\hat{L}(t)$ ) versus scale ( $t$ ) for canopy tree groups (all trees, conifer trees, deciduous trees) versus understory white spruce (*Picea glauca*) trees in all study plots in which both groups had at least 20 tree stems present. Solid lines are  $\hat{L}(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate aggregation, negative scores indicate segregation.

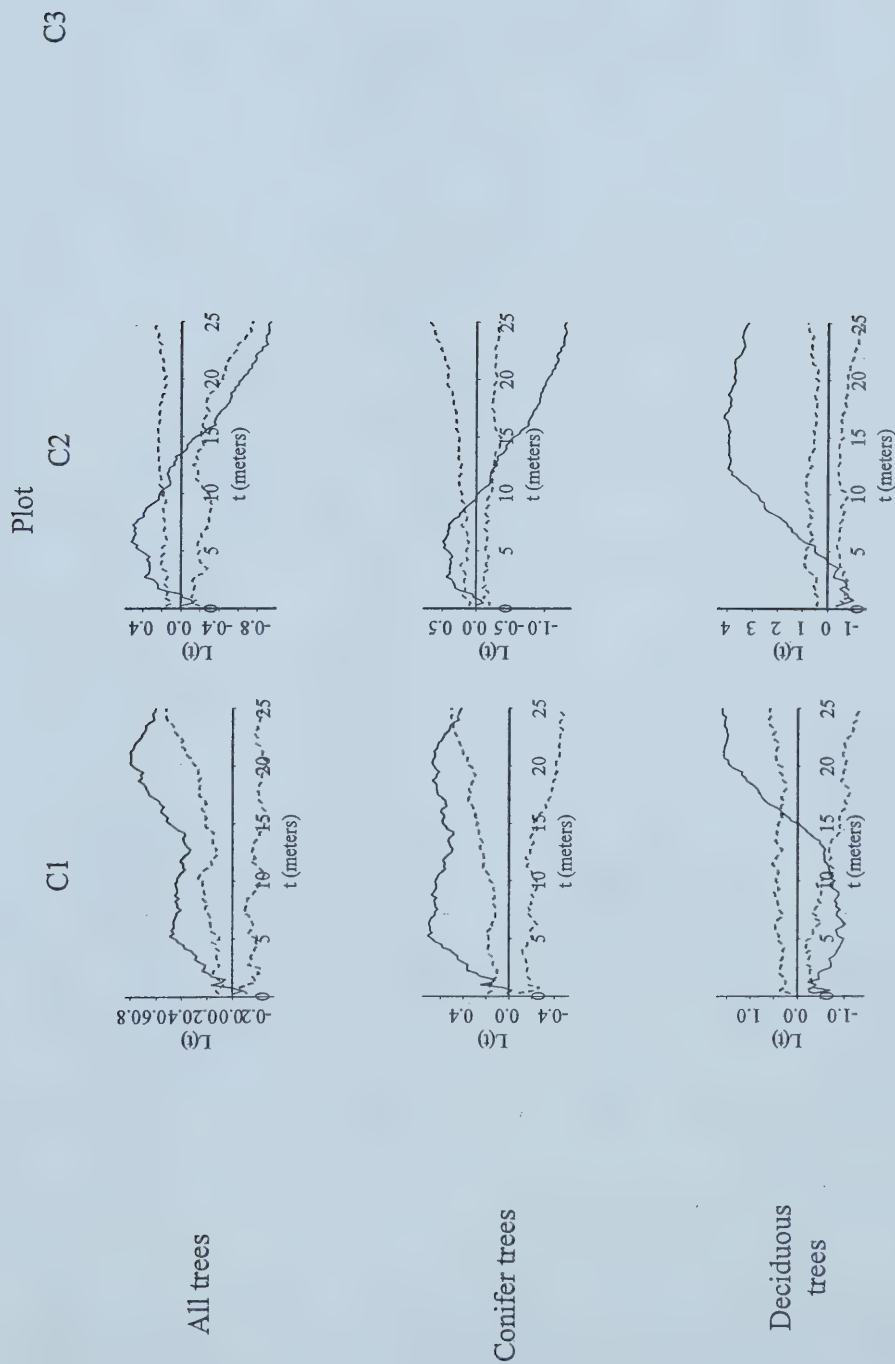




**Figure 2.6.** Plot of Ripley's bivariate K results ( $L(t)$ ) versus scale ( $t$ ) for canopy tree groups (all trees, conifer trees, deciduous trees) versus understory trembling aspen (*Populus tremuloides*) trees in all study plots in which both groups had at least 20 tree stems present. Solid lines are  $L(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate aggregation, negative scores indicate segregation.







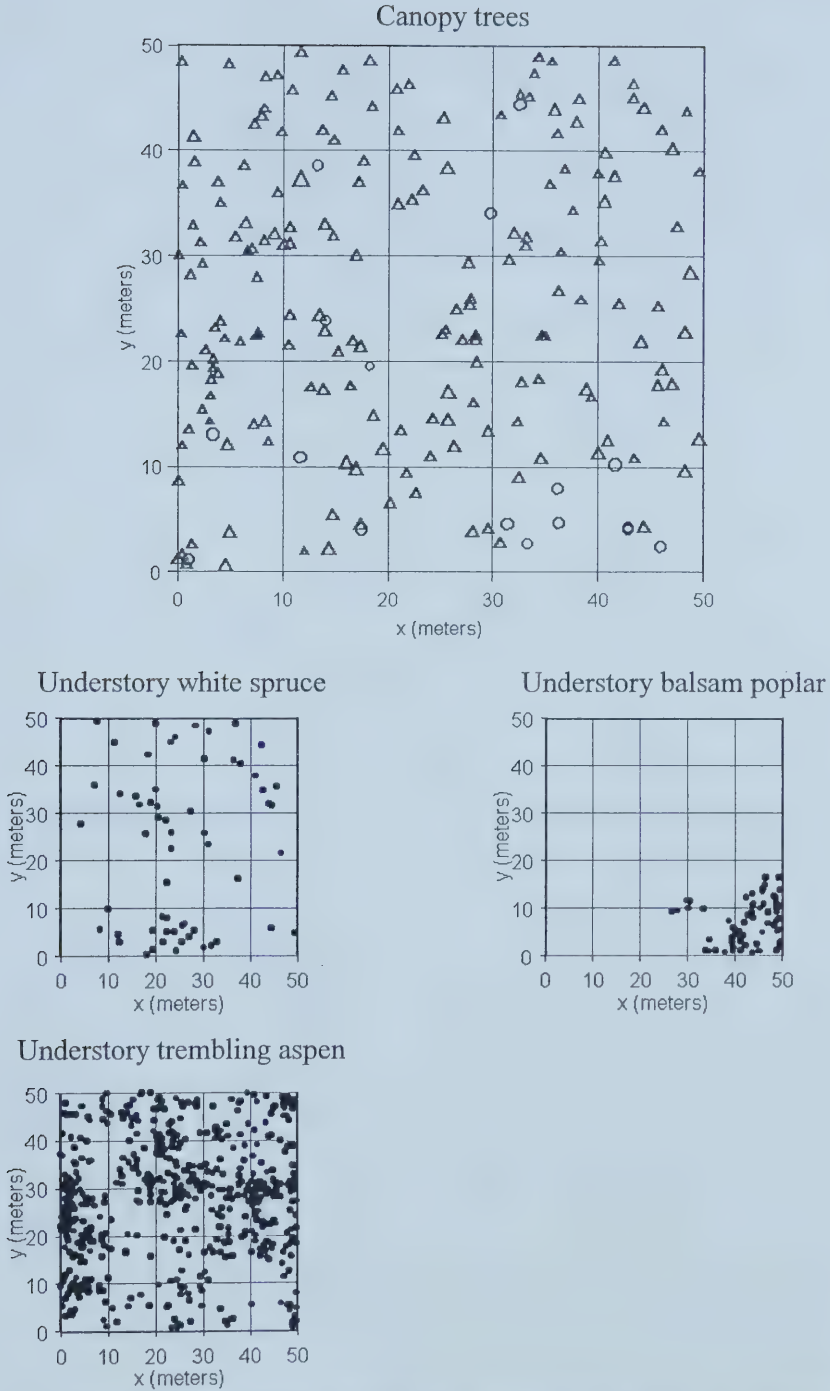
**Figure 2.6 continued.** Plot of Ripley's bivariate K results ( $L(t)$ ) versus scale ( $t$ ) for canopy tree groups (all trees, conifer trees, deciduous trees) versus understory trembling aspen (*Populus tremuloides*) trees in all study plots in which both groups had at least 20 tree stems present. Solid lines are  $L(t)$  scores, dotted lines are 95% confidence intervals. Positive scores indicate aggregation, negative scores indicate segregation.





**Figure 2.7.** Map of canopy (>10 meters tall) and understory tree (<10 meters tall) locations in plot C1. Circles in canopy tree plot are proportional to tree DBH, dark circles are canopy conifers, light triangles are canopy deciduous trees.

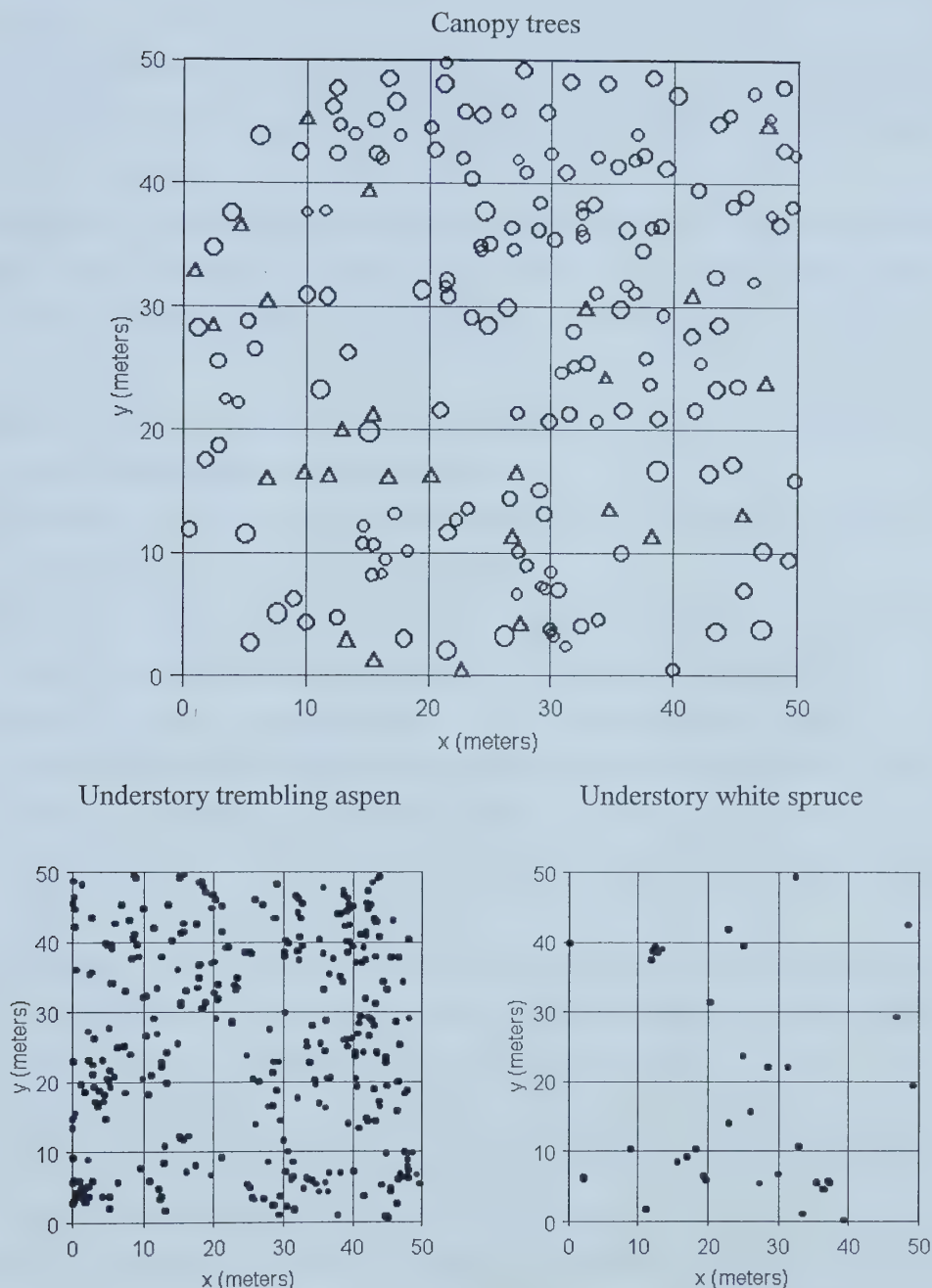




**Figure 2.8.** Map of canopy (>10 meters tall) and understory tree (<10 meters tall) locations in plot A2. Circles in canopy tree plot are proportional to tree DBH. Circles in canopy tree plot are proportional to tree DBH, dark circles are canopy conifers, light triangles are canopy deciduous trees.







**Figure 2.9.** Map of canopy (>10 meters tall) and understory tree (<10 meters tall) locations in plot M2. Circles in canopy tree plot are proportional to tree DBH. Circles in canopy tree plot are proportional to tree DBH, dark circles are canopy conifers, light triangles are canopy deciduous trees.



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### CHAPTER 3

## SMALL-SCALE SPATIAL STRUCTURE AND RELATION OF BOREAL MIXEDWOOD CANOPY AND UNDERSTORY VEGETATION

### Introduction

Plant communities are made up of a mosaic of vegetation patch types that change in relative abundance and distribution as they undergo successional change and interact with their environment (Watt 1947, Pickett and White 1985, van der Maarel 1996). The structure of, and relationship between, vegetation patches often varies with the spatial grain and extent of observation (Kotliar and Wiens 1990, Palmer 1990). Since different organisms in a community can sense and respond to their environment at different scales (Addicott et al. 1987, Wiens 1989), ecological studies which examine communities at several spatial scales simultaneously may provide new insights into the patterns and processes which structure those communities (Levin 1992).

Many studies have documented the spatial structure of forest canopies, and the importance of canopy structure and canopy gaps in determining patterns of understory tree regeneration, but few have examined the influence of canopy structure and canopy gaps on non-tree understory species biodiversity (Schnitzer and Carson 2000). In boreal forests, the majority of plant biodiversity is located not in the canopy, but in the understory. A rich assemblage of vascular plants, mosses and lichens can be found growing under a species-poor canopy which may contain an order of magnitude fewer species than the understory. Understory community diversity and composition at small spatial scales is controlled by numerous factors, including light availability, temperature, soil nutrient and moisture availability, dispersal limitation, competition, and herbivory (Collins et al. 1985, Dlott and Turkington 2000, Ehrlén and Eriksson 2000). Canopy trees and canopy gap environments can influence all of these factors, although few studies have been able to experimentally separate the different mechanisms of canopy influence on understory vegetation (Riegel et al. 1995).

Several studies have examined relationships between canopy and understory vegetation, but these studies have often focused on floristic relationships between forest



strata rather than structural relationships, or have measured canopy-understory structure and relationships at the stand or landscape scale (Carleton and Maycock 1981, McCune and Antos 1981, Gagnon and Bradfield 1986). At these scales, understory plant community cover, biomass, species richness and diversity may be related to the canopy cover type and tree density or basal area in a stand (Klinka et al. 1996, Stone and Wolf 1996, Pitkanen 1997, Brososke et al. 1999, Naumberg and DeWald 1999, McKenzie et al. 2000), as well as site edaphic variables such as soil type and moisture regime (Tonteri 1994), a fact which allows understory community composition to be used for ecological site type classification (Corns and Annas 1986). Understory non-vascular plant cover often increases with increasing canopy conifer cover during successional change, while understory vascular plants may respond differently to stand structure depending on their life-history strategy (Collins et al. 1985, Saetre et al. 1997, McKenzie et al. 2000). The abundance of shade-intolerant 'early successional' shrubs, forbs, graminoids and herbs often quickly decreases after canopy closure, while shade-tolerant 'late successional' species and non-vascular vegetation show the opposite trend (Carleton and Maycock 1980, Morneau and Payette 1989, de Grandpré et al. 1993, Saetre et al. 1997). The abundance and diversity of shrubs and early-successional herbaceous species often show stronger relationships with canopy cover than do late-successional species or mosses (McCune and Antos 1981, Klinka et al. 1996).

Although the stand and landscape scale structure and relationships between boreal canopy and understory vegetation are relatively well understood, few studies have examined the impact of small-scale boreal canopy structure on understory vegetation. Studies of the influence of canopy gaps on understory plant communities in tropical and temperate forests (Beatty 1984, Dirzo et al. 1992, Goldblum 1997, Svenning 2000) have demonstrated that understory biomass, cover and species richness are often higher under canopy gaps than adjacent closed canopy forest areas, although some studies have found no measurable response of understory vegetation to small experimentally created canopy gaps (Collins and Pickett 1988). Understory plants are able to respond to the availability of light, moisture and nutrients in canopy gaps by increasing vegetative and reproductive growth under gaps (Collins et al. 1985), although these increases may be short lived in





forests where canopy gaps are quickly closed by lateral growth of surrounding trees into gaps (Valverde and Silvertown 1998).

In boreal forests, areas under canopy gaps may have higher light levels and temperatures than those under a closed canopy (Canham et al. 1990, Lieffers et al. 1999). Canopy gap soils may contain higher amounts of nitrogen, lower amounts of phosphorous and potassium, higher decomposition rates and lower amounts of leaf litter than those found under a closed canopy (Paré et al. 1993), and treefalls which create canopy gaps may create tip-up mounds and areas of soil disturbance which can be rapidly colonized by understory species (Jonsson and Esseen 1990). A study in small experimental canopy gaps in the eastern boreal forest of Canada found that understory cover, diversity and species richness all increased after the creation of a canopy gap, often due to increases in cover of shrub and herb species already present in the gap (de Grandpré and Bergeron 1997). Older boreal forests showed a greater relative increase of understory plant cover and species richness after gap creation than young forests, and a greater proportion of the understory regeneration in these gaps was due to plants established from seed dispersed into the gap and the seed bank, rather than by increases in the cover of existing vegetation.

At small spatial scales, individual canopy trees can influence the vegetation growing beneath them through their effects on the availability of resources in the understory and through direct competition with understory plants. The nature and strength of tree influences on the understory varies between tree species (Canham et al. 1994, Pelletier et al. 1999). Conifers such as spruce and pine often dramatically decrease photosynthetically active radiation availability, decrease microbial biomass and activity, decrease soil moisture and pH, increase water throughflow due to stemflow and the canopy drip zone, and increase acidic needle litter deposition (Beatty 1984, Paré et al. 1993, Canham et al. 1994, Frego and Carleton 1995, Saetre et al. 1997, Økland et al. 1999, Pelletier et al. 1999, Saetre 1999). Deciduous trees such as birch, aspen and poplar may decrease photosynthetically active radiation availability (although not to the levels found under conifers), influence the availability of soil nitrogen, calcium, phosphorous, potassium, or sulfate, deposit leaf litter, and in some cases increase soil moisture availability due to stemflow (Beatty 1984, Crozier and Boerner 1984, Paré et al. 1993,



Pelletier et al. 1999, Saetre 1999). Individual understory species may have preferences for the microsite conditions found under particular canopy tree species (Crozier and Boerner 1984). Shade-intolerant vascular plant species may be found less often under canopy conifers than under deciduous trees or canopy gaps, while shade-tolerant mosses which require high moisture availability may be found under the drip zone of canopy conifers (Kuuluvainen and Pukkala 1989, Kuuluvainen et al. 1993, Økland et al. 1999).

Studies of the spatial structure of forest understories have generally found that understory species have patchy spatial distributions at small scales (Kuuluvainen et al. 1993, Fortin et al. 1999, Saetre 1999). Understory succession in boreal forests is thought to primarily involve the expansion and coalescence of existing patches of vegetation, with understory patch sizes and heterogeneity changing with stand age (Shafi and Yarranton 1973, Tonteri 1994, Fortin et al. 1999). Although the total species richness and diversity of the understory may not change significantly during succession, the size and spatial arrangement of patches of understory vegetation do change (Fortin et al. 1999). Despite the importance of the boreal understory in terms of its primary productivity, effects on tree regeneration, as wildlife habitat and as the most biologically diverse boreal plant stratum, few studies have quantified the small-scale spatial structure of the boreal understory, or examined the effects of canopy structure on understory community structure at small spatial scales.

The objectives of this study were to quantify the small-scale spatial structure of, and relationships between, boreal mixedwood canopy and understory vegetation, and to study differences in the spatial structure of boreal vegetation along a gradient of stand composition, from younger Aspen-dominated stands to older Mixed and Conifer-dominated stands. I also specifically examined differences in the influence of canopy conifers versus deciduous trees on understory vegetation patterns, and differences in spatial structure and relationships with canopy trees between vascular and non-vascular plant species.

## Methods



## *Data collection*

Vegetation data were collected during the summer of 1999. Four transects were established in the core area of each of the seven study plots described in Chapter 2, for a total of 28 transects, of which 12 were located in the Conifer dominated plots, 8 were located in Mixed canopy composition plots and 8 were established in Aspen dominated plots. Each 50 meter long transect consisted of 100 contiguous 0.5 meter by 0.5 meter square quadrats. In each plot, two transects were established running north-south and two running west-east. Start points of each transect were placed in a stratified random fashion, with one start point placed randomly in each half of the south and west edge of the core area of each plot. For recording purposes, the quadrats in each transect were numbered starting with the southernmost or westernmost quadrat in each transect. I also established an additional 121 quadrats in each plot in a grid layout, with quadrats spaced evenly every 5 meters throughout the plot.

For each quadrat, I visually estimated percent cover of all vascular and non-vascular plant species lying in or above the quadrat. I recorded cover estimates separately for canopy trees and understory vegetation. Canopy cover was measured as a visual estimate of percent of sky obscured by canopy trees and foliage above the quadrat. Cover of understory vegetation was estimated as vertically projected percent cover for each species present in the quadrat. Covers for both strata were measured to the nearest 1%. Plants were identified to species in the field when possible, or collected and identified in a herbarium when their identity was uncertain. Mosses and lichens growing on tree stems, decaying wood or stumps were not identified or included in cover estimates.

## *Data analysis*

### *Distribution maps*

Geostatistical techniques were used to construct maps of the estimated distribution of canopy and understory variables throughout each plot based on both grid quadrats and transects of quadrats in each plot. I summarized the spatial structure of each





variable using Cressie and Hawkins' (1980) robust semivariogram estimator, which estimates semivariogram values ( $\bar{\gamma}(h)$ ) for sample points separated by varying distances ( $h$ ). Spatially autocorrelated variables generally exhibit lower semivariogram estimates (lower variance between samples) for points which are closer together in space. For each variable, I fitted a semivariogram model to the empirical semivariogram estimates. Semivariogram models such as the spherical or exponential model possess several parameters such as the sill (total data variance), nugget (residual variance not explained by the spatial model), and the range (the distance at which spatial dependence is no longer observed in the data) (Rossi et al. 1992). Semivariogram models were used to create an estimated map of the distribution of each variable using ordinary kriging, which estimates values of a variable at any desired location in an area based on the values at sample locations and the spatial structure of the variable (Bailey and Gatrell 1995). All variables were square-root or log transformed prior to estimation of the empirical semivariograms and semivariogram models, and back-transformed for display of the kriged maps.

### *Multiscale analyses*

To examine relationships between canopy and understory vegetation at several spatial scales, I used wavelet analysis of the cover data for each transect. Wavelets are a family of mathematical functions which are widely used for pattern analysis in remote sensing, geophysics and computer vision (Chui 1992, Daubechies 1992, Schowengerdt 1997), and which have been applied in several recent studies of ecological patterns at a range of temporal and spatial scales (Bradshaw and Spies 1992, Clemen 1998, Dale and Mah 1998, Saunders et al. 1998, Broszofski et al. 1999, Mehlum et al. 1999). The type of wavelet analysis most commonly used in ecological studies is the continuous wavelet transform, which involves moving a windowing function (the 'wavelet') along a data set and assessing the match between wavelet and data at each point along the data train. A range of wavelet sizes is used, giving a transformation of the data by wavelet at several scales. This type of transformation is referred to as a scale-space transformation





(Schowengerdt 1997), because a transform value is generated for all desired combinations of scale and spatial location of the analyzing wavelet.

The continuous wavelet transform value  $W$  at point  $x_i$  for scale of analysis  $b_k$  is described by the equation:

$$W(b_k, x_i) = \frac{1}{b_k} \sum_{j=1}^n y(x_j) g((x_j - x_i)/b_k) \quad (3.1)$$

The function  $y(x)$  is the data value at point  $x$ , and  $g(x)$  is the analyzing wavelet function. This equation states that a wavelet function is moved along the data series and the match between data and analyzing wavelet is calculated at each position. This process is repeated for a range of wavelet sizes, from very small to relatively large. Positive wavelet transform values indicate a good match between wavelet and data, and negative scores represent a poor match between wavelet and data. For certain wavelet functions such as the Sombrero wavelet, extreme values of the wavelet transform correspond to structures in the data such as patches or gaps. Positive wavelet transform values indicate patches in the data, and negative wavelet transform values indicate gaps.

Wavelet analysis was used to determine scales of spatial pattern for several canopy and understory variables, including total canopy cover, coniferous canopy cover, total understory species richness ( $S$ ) and Shannon diversity ( $H'$ ), total cover of understory vascular and non-vascular plants, ordination scores of each quadrat on the first axis of a detrended correspondence analysis (DCA) performed on the cover of understory species in all quadrats using PC-ORD software (McCune and Mefford 1999), and for the cover of the individual understory species *Rosa acicularis*, *Linnaea borealis* and *Hylocomium splendens*, which were common in all seven study plots. The ordination was performed using percent cover estimates for all understory species which occurred in at least 20 of the 3647 quadrats sampled.

All analyses were performed using the Sombrero (or 'Mexican Hat') wavelet function, which has been widely used in ecology due to its ability to smooth noisy data and detect patches and gaps at a range of spatial scales (Bradshaw and Spies 1992, Dale



and Mah 1998, Saunders et al. 1998 Brosofske et al. 1999), and is described by the equation:

$$g(x) = \frac{2}{3^{0.5}} \pi^{-0.25} (1 - 4x^2) e^{-2x^2} \quad (3.2)$$

where  $x$  is the relative distance from the centre of the analyzing wavelet, scaled by the spatial scale of analysis (see equation 3.1). For all variables in each transect the wavelet variance was calculated for spatial scales from 0.5 to 15 meters using the equation:

$$V_w(b_k) = \sum_{i=1}^n W^2(b_k, x_i) / n \quad (3.3)$$

The resulting plot of wavelet variance versus scale (the ‘scalogram’) is analogous to the variance plots used in techniques such as two- or three-term local quadrat variance, with peaks or shoulders in the wavelet variance at a particular scale indicating the dominant scales of pattern in the data (Dale and Mah 1998). In addition, I calculated the covariance between canopy variables and all understory variables at all scales in each transect using the formula (Greig-Smith 1983):

$$C_{CU}(b_k) = (V_{C+U}(b_k) - V_C(b_k) - V_U(b_k)) / 2 \quad (3.4)$$

where  $C_{CU}$  is the canopy-understory wavelet covariance at scale  $b_k$ , and  $V_C$ ,  $V_U$  and  $V_{C+U}$  are the wavelet variances of the canopy, understory, and canopy and understory combined respectively. Peaks or shoulders in the covariance scalograms indicate the spatial scales at which there are relationships between canopy and understory variables.

Wavelet analysis in ecology has generally been used in a descriptive fashion, without any testing for the statistical significance of observed patterns. Since I was interested in comparing scales of pattern in variance and covariance between transects and plot types, I used randomization procedures (Manly 1991) to determine if the



observed wavelet variances and covariances were significantly different from those expected from completely spatially random variables.

For all variables and transects, I randomly shuffled values within the transect for each variable and recalculated wavelet variances and covariances at each scale. This process was repeated 1000 times for each variance/covariance, and the observed variance/covariance values were compared to the randomly generated values to obtain a randomized p-value based on the number of times in 1000 randomizations the randomly generated values were greater than the observed values (Legendre and Legendre 1998):

$$p = \frac{(\# \text{ randomized values greater than observed value}) + 1}{\# \text{ randomizations}} \quad (3.5)$$

Variance/covariance peaks and shoulders were judged to be significant if the p-value at the scale of a peak or shoulder was less than or equal to 0.05. The spatial scale of all significant peaks and shoulders were tallied for each variable and combination of variables.

## Results

### *Inter-Plot Patterns*

Understory plant community structure was highly variable between and within study plots. The first axis of the DCA ordination of the understory data explained 12% of the variation in the data set, and was highly correlated with canopy cover type (Figure 3.1). Quadrat scores on the first DCA axis were correlated with increasing trembling aspen canopy cover ( $r = 0.550$ ) and decreasing white spruce canopy cover ( $r = -0.491$ ). The second and third axes of the ordination explained 8% and 6% of the variation in the data set, respectively, and were not significantly correlated with any canopy cover variables. Understory species with positive scores on the first axis were mostly ‘early-successional’ species characteristic of Aspen-dominated stands, while species with negative scores were ‘late-successional’ species characteristic of Conifer-dominated



stands (Table 3.1). Mean vascular plant cover, understory species richness and diversity, and ordination scores were higher overall in Aspen-dominated plots, while non-vascular plant cover was higher overall in Mixed and Conifer-dominated plots.

### ***Intra-Plot Patterns***

The range of spatial dependence of the variables examined in this study ranged from less than 2 meters to greater than 30 meters (Table 3.2). The spatial structure of variation in these variables was well described by the semivariogram models, as shown by the good fit of most of the semivariogram models to the empirical semivariogram estimates (Figures 3.2 and 3.3). The spatial structure of the environment is often hierarchical in nature, making it difficult to fit traditional spatial models such as the semivariogram to empirical data collected over large spatial extents (O'Neill et al. 1991). The limited extent of spatial scales examined in this study made the use of these methods more appropriate, since it is likely that spatial effects at small spatial scales can be adequately modeled by simple semivariograms. As the kriged maps of each plot indicated (Figures 3.4-3.11), all variables were patchy in their small-scale spatial distribution.

The accuracy of maps of predicted understory species distributions was strongly influenced by the semivariogram model used to estimate values throughout the plot. Although each plot was covered by a grid of quadrats spaced 5 meters apart in addition to the transects, for variables with a range of spatial dependence less than 5 meters, the kriged cover estimates at points with no quadrats nearby were much less precise than for points adjacent to a sample location. The 5 meter spacing of the grid quadrats was chosen based on an initial assessment of the range of spatial dependence in one study plot, but clearly the highly variable nature of spatial dependence in these plots resulted in mapped estimates of some variables showing high standard errors, due to many points in the plot not being within the range of spatial dependence of a sample plot for that variable. Maps of variables with ranges of spatial dependence less than 5 meters were visibly affected by the location of sample points, a symptom of inadequate sampling. However, tradeoffs between the need to adequately sample numerous plots versus the need to sample some plots at very fine spatial scales to capture all scales of spatial variation, and the fact that





the majority of variables showed ranges of spatial dependence greater than 5 meters, made the sampling layout used for this study adequate in most cases. These maps were useful for a qualitative assessment of the general spatial distribution of variables in each plot.

A visual examination of the distribution of canopy and understory variables in the study plots (Figures 3.4-3.11) indicated several obvious trends. Understory vascular plant cover and understory species richness appeared to be negatively associated with conifer tree cover in most plots. In Conifer and Mixed plots, these variables seem to be positively associated with both canopy gaps and areas of deciduous tree cover. In contrast, understory non-vascular plant cover often appeared to be positively associated with canopy conifer tree cover. Understory quadrat ordination scores were higher overall in Aspen dominated plots, but within Mixed and Conifer plots, were generally relatively high in canopy gaps and under individual deciduous trees, and low throughout the rest of the plot.

Understory vascular plants occurred more frequently and were generally more widespread and less patchy in their occurrence in Conifer and Mixed plots than in Aspen plots, while the opposite was true for non-vascular plants, which tended to occur much less frequently and in smaller patches in the Aspen dominated plots.

### *Multiscale analyses*

All measured variables exhibited significantly non-random spatial patterns of patch or gap structure in at least one transect. I summarized the spatial patterns of each canopy and understory variable as the proportion of transects in each of the three plot types (Aspen, Mixed and Conifer) which exhibited significant variances or covariances in a particular range of spatial scales (Figures 3.12 and 3.13).

### *Significant wavelet variances*

A summary of the total number of significant variance peaks at particular scales for each variable across all 28 transects (Figure 3.12) indicated that total cover of canopy



trees and cover of coniferous canopy trees had significantly non-random patches and gaps at all scales. Both variables showed the most peaks at scales of 5 - 7.5 meters, but peaks at larger scales were also common. Total canopy cover showed slightly more peaks than coniferous canopy cover.

Total cover of understory vascular and non-vascular plants also showed patchiness at all scales. Scales of pattern in the vascular vegetation tended to be larger than those found in the non-vascular vegetation. Quadrat scores from the first axis of a DCA ordination of the combined understory data showed patterns at scales of 2.5 - 5 meters and at scales larger than 7.5 meters. Species richness and diversity showed similar patterns with peaks at all scales greater than 2.5 meters, and most peaks at a scale of around 10 - 12.5 meters.

Results for the understory shrub *Rosa acicularis* showed significant peaks mostly at scales greater than 10 meters, while the dwarf shrub *Linnaea borealis* and the moss *Hylocomium splendens* had higher numbers of significant peaks, which tended to occur at smaller scales less than 10 meters in size. Significant peaks were more common for individual species than for total cover or richness measures of the understory strata.

### *Significant wavelet covariances*

Covariances between canopy and understory variables also showed significant peaks at a range of scales (Figure 3.13). The number and spatial scale of covariances were usually similar for both canopy variables, with coniferous canopy cover generally covarying with understory variables at larger scales than total canopy cover.

Canopy – understory covariances tended to occur at larger scales for understory vascular vegetation than non-vascular vegetation. Ordination scores covaried with total canopy cover more commonly than with coniferous canopy cover, but generally showed significant covariance with coniferous canopy cover at larger scales. Significant covariance between canopy cover and species richness were very uncommon, occurring only in a few transects, and more commonly occurring with coniferous canopy cover than total canopy cover. There were no significant covariances between canopy cover and understory species diversity.



The majority of canopy-understory covariances were negative, although positive covariances were more common between total canopy cover and understory variables than between conifer canopy cover and understory variables (Table 3.3). Positive covariances were common between conifer canopy cover and non-vascular plant cover at larger scales, and between total canopy cover and ordination scores.

Canopy covariances with individual understory species were generally more prevalent at larger scales. *Hylocomium splendens* showed more significant covariance peaks with the canopy than *Linnaea borealis* or *Rosa acicularis*, and these peaks were distributed fairly evenly among scales greater than 2.5 meters. *Linnaea borealis* and *Rosa acicularis* showed more peaks at larger scales, and significant covariances with coniferous canopy were more common than those with total canopy cover.

Most covariances between canopy variables and *Hylocomium splendens* cover were negative at very small scales and positive at larger scales, while negative covariances between canopy variables and *Linnaea borealis* and *Rosa acicularis* were prevalent at all scales (Table 3.3).

#### *Significant wavelet variances – differences between plot types*

A breakdown of the percentage of transects in each of the three plot types (Aspen, Mixed, Conifer) indicated that there were differences in the prevalence of patch/gap structure in the vegetation strata in these plot types (Figure 3.12). Significant peaks in total canopy cover were prevalent in all plot types, but were slightly more common in Mixed and Conifer dominated plots. As might be expected, significant conifer canopy cover peaks were much more common in Mixed and Conifer dominated plots, but they did occur in a few Aspen dominated plots, and tended to occur at small scales (< 7.5 meters) when present in these plots.

Significant structure in understory vascular and non-vascular plant cover was less common in the Aspen dominated transects. When present, significant variance peaks in non-vascular vegetation cover in the Aspen dominated transects were at small scales (< 7.5 meters), as were peaks in the ordination scores. Peaks in understory species richness





and diversity were most common in the Mixed transects, and least common in the Aspen dominated transects.

Significant patch/gap structure in individual species' covers were common in all plot types. Cover of *Hylocomium splendens* generally showed significant peaks at smaller scales in the Aspen dominated plots, as did the cover of *Linnaea borealis*. The opposite was true for *Rosa acicularis*, which showed more peaks at larger scales in the Aspen and Mixed transects.

### *Significant wavelet covariances – differences between plot types*

Significant covariance peaks between canopy variables and understory vascular and non-vascular plant cover and ordination scores were not found in any Aspen dominated transects, but were found in most Mixed and Conifer dominated transects (Figure 3.13). The few significant covariances between canopy cover and understory species richness were found at larger scales for the Mixed and Conifer dominated plots than the Aspen dominated plots.

Covariances between total canopy cover and understory vascular and non-vascular vegetation were mostly negative in Conifer dominated plots, but occasionally positive at large scales in the Mixed plots (Table 3.3).

There were no significant covariances between total canopy cover and *Hylocomium splendens* or *Linnaea borealis* cover in the Aspen dominated transects, but covariances between canopy and cover of these species were common in the Mixed and Conifer dominated plots (Figure 3.13). Covariances between coniferous canopy tree cover and these two species were found in some Aspen dominated transects. *Rosa acicularis* cover covaried with canopy variables more often in the Conifer and Mixed transects.

A greater proportion of significant covariances between canopy variables and *Hylocomium splendens* cover were positive in the Conifer dominated plots than the Mixed plots. *Rosa acicularis* covariances with canopy variables were generally negative, especially in the Conifer plots (Table 3.3).





## Discussion

The distributions of boreal mixedwood canopy and understory vegetation were patchy at several spatial scales. Many of the patterns I observed were found only at certain spatial scales, and the nature and strength of canopy-understory relationships varied with the scale of observation. For example, understory non-vascular plant cover was frequently negatively related to conifer canopy cover at very small spatial scales, but positively related to conifer canopy cover at larger spatial scales. A multi-scale approach to the analysis of ecological data can provide insights that might be overlooked by analyses carried out at a single spatial scale.

Canopy conifers such as white spruce appeared to have a much greater influence on the distribution of understory vegetation than canopy deciduous trees such as trembling aspen. This trend was apparent both from the larger number of covariances between conifer canopy cover and understory vegetation than between total canopy cover and understory vegetation, and from the fact that canopy-understory relationships were much more common in Mixed and Conifer-dominated plots where conifers made up the majority of the canopy (Figure 3.13). This trend is probably related to the ability of canopy conifers to reduce light levels well below those found under canopy deciduous trees (Canham et al. 1994, Lieffers and Stadt 1994), as well as the differences in leaf litter deposition, soil nutrients and moisture availability under canopy conifers versus canopy deciduous trees (Paré et al. 1993, Økland et al. 1999, Pelletier et al. 1999, Sætre 1999). Understory vascular vegetation cover was much higher in canopy gaps and under deciduous trees than under conifer trees, while non-vascular vegetation cover was higher under conifer trees. This pattern was especially obvious in Aspen-dominated plots, where the few mosses present in these plots were frequently found growing under isolated conifer trees.

Succession in boreal mixedwood forests usually proceeds from initial dominance of a stand by shade-intolerant species such as aspen and poplar, towards increasing canopy dominance by shade-tolerant species such as spruce and fir (Dix and Swan 1971, Carleton and Maycock 1980, Morneau and Payette 1989, de Grandpre et al. 1993, de Grandpre and Bergeron 1997, Fortin et al. 1999, Bergeron 2000). The oldest living trees



in the Aspen dominated plots were approximately 80 years old, while the oldest trees in the Mixed and Conifer dominated plots were between 100 and 150 years old (Table 2.1). The age of the oldest trees in a stand may be a biased estimator of true stand age, especially in older stands where continuous canopy replacement may be occurring after a major disturbance, but the age of the oldest living trees in the stand at any point in time will be limited by tree life-span rather than stand age (Cumming et al. 2000). The age of the oldest living tree in a stand may not be indicative of the actual age of the stand, but information on the time since major disturbance was not available for the plots used in this study. Although aspen and poplar may persist in the canopy for extended periods of time in the absence of conifer tree propagule availability (Cumming et al. 2000), in this study I assumed that the Aspen dominated plots were representative of an earlier successional stage than Mixed and Conifer dominated plots. Changes in canopy composition may take extended periods of time, so it is unlikely that the Aspen plots I surveyed will become Mixed or Conifer dominated in the immediate future, but in the absence of stand-initiating disturbance, it is likely that their canopy composition will become increasingly dominated by conifers as succession proceeds.

Aspen dominated plots showed much more homogenous understory communities, with higher mean cover and a more homogenous community composition throughout the plots. In Mixed and Conifer dominated plots, understory community cover and composition was much more heterogenous and patchily distributed, and the scale of patchiness was larger than in the Aspen dominated plots. Understory vascular plant cover was much higher in canopy gaps in these plots, while non-vascular plant cover (composed mostly of feather mosses) changed from the isolated patches found under conifers in the Aspen plots, to large patches found throughout the plot. Understory community composition in canopy gaps in the Mixed and Conifer plots is similar to the community composition found in Aspen dominated plots, as shown by the high ordination scores found in both Aspen plots, and in regions of low canopy cover in Mixed and Conifer plots.

These results are consistent with previous findings that change in understory community composition during succession in boreal forests is driven by changes in the spatial arrangement of existing understory species patches (Watt 1947, Shafi and



Yarranton 1973, Fortin et al. 1999, van der Maarel 1999), rather than by total replacement of species as predicted by a relay floristics model of succession (Egler 1954). Most boreal understory species are found in a range of stand types and stand successional ages, but their relative abundances and spatial distributions change as environmental conditions in the understory are modified by canopy and soil development (Shafi and Yarranton 1973, Carleton and Maycock 1980, Morneau and Payette 1989, de Grandpré et al. 1999, Fortin et al. 1999).

Yarranton and Morrison (1974) documented a pattern of patch dynamics during primary succession on sand dunes, where small patches of pioneer species grow via nucleation from isolated colonization points to cover a site, until invader species appear later in succession and expand via nucleation to cover the site, while the pioneers are again reduced to a patchy cover amongst a matrix of invader cover. In the Aspen-dominated plots in this study, vascular plants form a relatively homogenous cover throughout the plot, while mosses are present in small patches. In forests where conifer canopy cover is higher, vascular plant cover is greatly reduced except in patches of high cover found under canopy gaps, while moss cover is more homogenous and feather mosses are found throughout the plot. If the assumption that Aspen-dominated stands generally represent an earlier stage of succession in boreal forests is correct, the results of this study may indicate that changes in canopy composition and environmental conditions in boreal forests create a pattern of understory community change during secondary succession that is similar to the pattern of nucleation and patch expansion seen in other ecosystems undergoing primary and secondary succession (Yarranton and Morrison 1974, Shafi and Yarranton 1973, Dale and Blundon 1990, Dale and Blundon 1991, Fortin et al. 1999).

This study was not able to address the influence of gap age on understory composition. In experimental canopy gaps in the eastern boreal forests of Canada, understory plant cover and species richness increased rapidly after gap creation, but often stabilized at a new higher mean value in the gap within 4 years (de Grandpré and Bergeron 1997). I found many significant relationships between canopy cover and understory covers, but very few significant relationships between canopy cover and understory species richness or diversity. The results in this study were otherwise





consistent with those found in eastern boreal forests, and it is possible that the rate of gap formation in the study plots was slow enough to have allowed understory vegetation to come to an equilibrium with existing levels of canopy cover. De Grandpré and Bergeron (1997) noted that change in understory composition in gaps, relative to pre-disturbance conditions, increased with increasing stand age and conifer presence in the canopy. I found a similar pattern, with understory community composition differing greatly between gaps versus non-gaps in the Conifer and Mixed plots, while community cover and composition were much more homogenous in the Aspen dominated plots. The high vascular plant covers and ordination scores found throughout Aspen-dominated plots were found only under canopy gaps in the Mixed and Conifer-dominated plots.

The randomization approach used for significance testing in this study proved useful for comparing observed patterns to those expected by chance, and for combining results from numerous transects. One problem encountered with this randomization approach was that the method used to shuffle data values when generating randomized variances and covariances made some unrealistic assumptions about the structure of the data. I completely shuffled both variables for each randomization. This was a valid approach when computing significances of wavelet variance scores, since I was interested in comparing observed patterns with those expected from spatially random data. When computing covariances between variables, this method examined spatial relationships between variables, but assumed that each variable is spatially random (Fortin and Jacquez 2000). This was clearly not the case since I observed significantly non-random spatial patterns in most variables. The result of this violated assumption is that the statistical tests of wavelet covariances may have been too liberal. Several proposed solutions for this problem, such as deflation of the test statistic, shift-based randomization procedures or Monte Carlo approaches (Fortin and Jacquez 2000, Dale and Fortin unpublished manuscript), were difficult to implement given the already demanding computational requirements of the wavelet randomization method, and the relatively short transect length sampled in this study. Thus, the wavelet covariance results need to be interpreted with caution since they may have overestimated the significance of some results, although most significant covariance peaks were extremely significant ( $p \leq 0.001$ ), which





may indicate that significant results were not simply artifacts of an overly liberal statistical test.

## Conclusions

The results reported in this study indicated that boreal mixedwood canopy and understory vegetation was patchily distributed at a range of small spatial scales. Understory vegetation was generally patchier in Mixed and Conifer forests with increased conifer presence in the canopy, and conifer trees appeared to have a greater influence on the distribution of understory vegetation than deciduous trees did. Understory vascular plant cover was higher under canopy gaps than under closed canopies at a range of spatial scales, while understory non-vascular plant cover was lower under canopy conifer trees at very small spatial scales, and higher under canopy conifer trees at larger spatial scales.

Estimates of canopy cover are a surrogate measure for the influence of the canopy on the understory environment. I did not address the specific mechanisms which caused the observed relationships between canopy and understory vegetation. Many factors other than canopy structure and composition play a role in structuring boreal understory plant communities. Soil type, moisture and nutrient availability, herbivory, soil disturbance, dispersal limitation and competition can all contribute to distribution of understory species at spatial scales from the local to the regional. I did not measure any of these variables, and further studies which examine variables other than canopy cover would be useful for determining the processes which gave rise to the patterns and relationships I observed, as well as accounting for variation in the spatial patterns of understory vegetation which was not explained by canopy cover. It would also be very useful to link studies of the small-scale spatial structure of boreal forest vegetation to studies at the stand and landscape scales to determine how processes operating at a larger range of spatial scales interact to determine patterns of boreal plant biodiversity.



**Table 3.1.** Understory species from 3674 sample quadrats at the EMEND study site ranked in order of their score on the first axis of a DCA ordination of all understory species present in at least 20 quadrats.

Species Name	Abbreviated Name	Axis 1 Ordination Score
<i>Symphoricarpos occidentalis</i>	Sym occ	479
<i>Thalictrum dasycarpum</i>	Tha das	460
<i>Aster ciliolatus</i>	Ast cil	445
<i>Moss species</i>	Moss sp	438
<i>Moss species</i>	Moss sp	437
<i>Vicia americanum</i>	Vic ame	429
<i>Moss species</i>	Moss sp	429
<i>Achillea millefolium</i>	Ach mil	425
<i>Epilobium angustifolium</i>	Epi ang	400
<i>Shepherdia canadensis</i>	She can	396
<i>Lonicera dioica</i>	Lon dio	393
<i>Fragaria virginiana</i>	Fra vir	372
<i>Actaea rubra</i>	Act rub	364
<i>Brachythecium salebrosum</i>	Bra sal	364
<i>Populus balsamifera</i>	Pop bal	361
<i>Galium boreale</i>	Gal bor	359
<i>Osmorhiza depauperata</i>	Osm dep	357
<i>Lathyrus ochroleucus</i>	Lat och	354
<i>Cladonia species</i>	Cla spp	343
<i>Rubus idaeus</i>	Rub ida	333
<i>Pyrola asarifolia</i>	Pyr asa	324
<i>Salix species</i>	Salix sp	313
<i>Delphinium glaucum</i>	Del gla	312
<i>Calamagrostis canadensis</i>	Cal can	300
<i>Viburnum edule</i>	Vib edu	285
<i>Ribes oxycanthoides</i>	Rib oxy	252
<i>Mertensia paniculata</i>	Mer pan	246
<i>Petasites palustris</i>	Pet pal	241
<i>Elymus innovatus</i>	Ely inn	236
<i>Populus tremuloides</i>	Pop tre	228
<i>Moss species</i>	Moss sp	222
<i>Rosa acicularis</i>	Ros aci	219
<i>Ribes triste</i>	Rib tri	202
<i>Lathyrus venosus</i>	Lat ven	202
<i>Aster conspicuus</i>	Ast con	189
<i>Cornus canadensis</i>	Cor can	188



**Table 3.1 continued.** Understory species from 3674 sample quadrats at the EMEND study site ranked in order of their score on the first axis of a DCA ordination of all understory species present in at least 20 quadrats.

Species Name	Abbreviated Name	Axis 1 Ordination Score
<i>Moneses uniflora</i>	Mon uni	186
<i>Plagiomnium cuspidatum</i>	Pla cus	185
<i>Rubus pubescens</i>	Rub pub	185
<i>Moss species</i>	Moss sp	174
<i>Pyrola secunda</i>	Pyr sec	171
<i>Carex species</i>	Carex	169
<i>Picea glauca</i>	Pic gla	161
<i>Moss species</i>	Moss sp	160
<i>Viola species</i>	Vio spp	158
<i>Dicranum species</i>	Dic spp	150
<i>Vaccinium caespitosum</i>	Vac cae	148
<i>Abies balsamea</i>	Abi bal	147
<i>Equisetum pratense</i>	Equ pra	139
<i>Mitella nuda</i>	Mit nud	138
<i>Arnica cordifolia</i>	Arn cor	135
<i>Galium triflorum</i>	Gal tri	135
<i>Habenaria orbiculata</i>	Hab orb	128
<i>Carex species</i>	Carex sp	111
<i>Linnaea borealis</i>	Lin bor	107
<i>Carex species</i>	Carex sp	107
<i>Equisetum arvense</i>	Equ arv	106
<i>Peltigera aphthosa</i>	Pel aph	102
<i>Maianthemum canadense</i>	Mai can	97
<i>Goodyera repens</i>	Goo rep	94
<i>Astragalus americanum</i>	Ast ame	91
<i>Ledum groenlandicum</i>	Led gro	83
<i>Vaccinium vitis-idaea</i>	Vac vit	83
<i>Equisetum sylvaticum</i>	Equ syl	81
<i>Dicranum species</i>	Dic sp	62
<i>Equisetum scirpoides</i>	Equ sci	59
<i>Hylocomium splendens</i>	Hyl spl	54
<i>Pleurozium schreberi</i>	Ple sch	48
<i>Pyrola virens</i>	Pyr vir	7
<i>Lycopodium annotinum</i>	Lyc ann	2
<i>Geocaulon lividum</i>	Geo liv	-4
<i>Ptilium crista-castrensis</i>	Pti cri	-22
<i>Carex species</i>	Carex sp	-49
<i>Dicranum polysetum</i>	Dic pol	-56



**Table 3.2.** Summary of semivariogram model types and ranges of spatial dependence fit to canopy and understory variables measured in seven study plots at the EMEND study site.

Plot	Canopy				Understory			
	Conifer Tree Cover		Deciduous Tree Cover		Vascular Plant Cover		Non-vascular Plant Cover	
	Model	Range (m)	Model	Range (m)	Model	Range (m)	Model	Range (m)
A1	n/a		Exponential	8.3	Spherical	8.7	Spherical	3.0
A2	Spherical	12.4	Spherical	10.1	Exponential	2.1	Spherical	12.8
M1	Exponential	3.9	Spherical	16.1	Exponential	2.1	Exponential	3.9
M1	Spherical	20.0	Spherical	19.4	Exponential	7.8	Exponential	1.5
C1	Exponential	6.8	Exponential	31.5	Exponential	6.1	Spherical	20.3
C2	Spherical	10.6	Linear	-	Spherical	8.0	Exponential	2.2
C3	Exponential	7.1	n/a		Exponential	3.1	Exponential	1.5

Plot	Understory				Understory			
	Ordination Scores		<i>Hylocomium splendens</i> cover		<i>Linnaea borealis</i> cover		<i>Rosa acicularis</i> cover	
	Model	Range (m)	Model	Range (m)	Model	Range (m)	Model	Range (m)
A1	Spherical	3.0	Spherical	0.5	Spherical	4.2	Spherical	9.8
A2	Exponential	4.6	Spherical	12.1	Spherical	33.0	Spherical	4.4
M1	Spherical	6.0	Spherical	4.3	Spherical	6.5	Spherical	5.6
M2	Spherical	20.0	Spherical	3.0	Spherical	8.6	Exponential	27.8
C1	Spherical	30.0	Spherical	5.7	Spherical	7.6	Spherical	18.9
C2	Exponential	2.3	Spherical	15.0	Exponential	2.4	Spherical	10.2
C3	Spherical	5.0	Exponential	6.0	Spherical	12.1	Spherical	5.5





**Table 3.3.** Proportions of transects in three stand types exhibiting significant negative and positive wavelet covariances between canopy and understory variables.

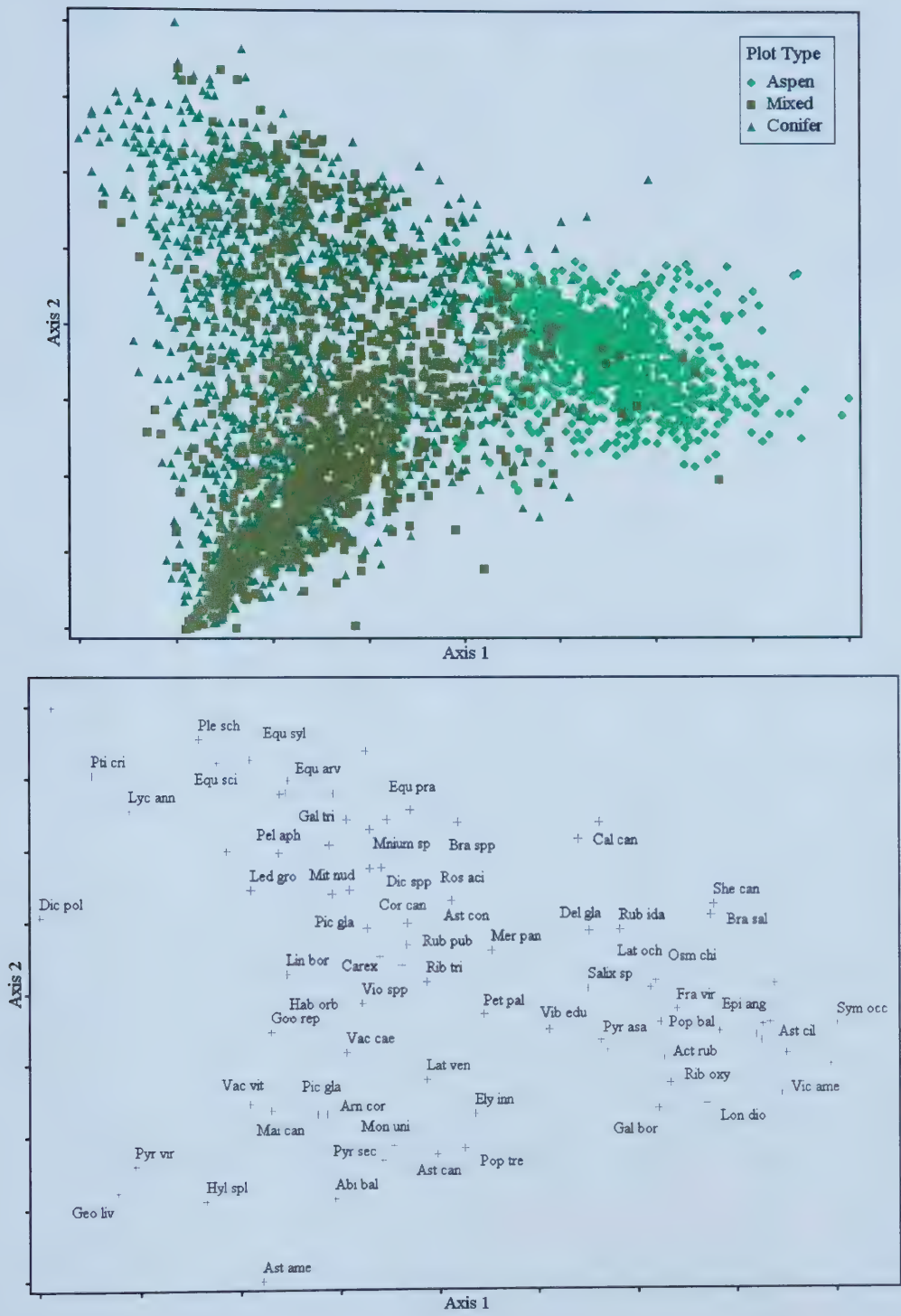
Variables	Stand Type	Proportion of transects in each stand type with negative covariance peaks at a given spatial scale						Proportion of transects in each stand type with positive covariance peaks at a given spatial scale					
		Scale (meters)						Scale (meters)					
		0-2.5	2.5-5	5-7.5	7.5-10	10-12.5	12.5-15	0-2.5	2.5-5	5-7.5	7.5-10	10-12.5	12.5-15
Total canopy cover vs.	Aspen												
	Mixed		0.13			0.13	0.13				0.25	0.13	
Vascular plant cover	Conifer		0.08	0.08	0.08	0.25	0.25		0.08	0.08	0.08		0.08
Total canopy cover vs.	Aspen												
	Mixed						0.13				0.13	0.13	0.13
Non-vascular plant cover	Conifer			0.33		0.08	0.33			0.08	0.08		
Total canopy cover vs.	Aspen					0.25			0.13			0.13	
	Mixed					0.25							
Ordination scores	Conifer			0.08		0.25	0.08			0.17	0.08	0.13	0.25
Total canopy cover vs.	Aspen												
	Mixed												
Species richness (S)	Conifer					0.08							
Total canopy cover vs.	Aspen												
	Mixed												
Species diversity (H')	Conifer												
Total canopy cover vs.	Aspen			0.38	0.13		0.13			0.13	0.13	0.13	0.13
	Mixed												
<i>Hylocomium splendens</i> cover	Conifer		0.08	0.17		0.08	0.08		0.17	0.08	0.25	0.08	0.33
Total canopy cover vs.	Aspen												
	Mixed									0.13			
<i>Linnaea borealis</i> cover	Conifer			0.17		0.08	0.17				0.17		
Total canopy cover vs.	Aspen					0.13							
	Mixed												
<i>Rosa acicularis</i> cover	Conifer			0.08	0.17		0.08					0.13	0.08



**Table 3.3 continued.** Proportions of transects in three stand types exhibiting significant negative and positive wavelet covariances between canopy and understory variables.

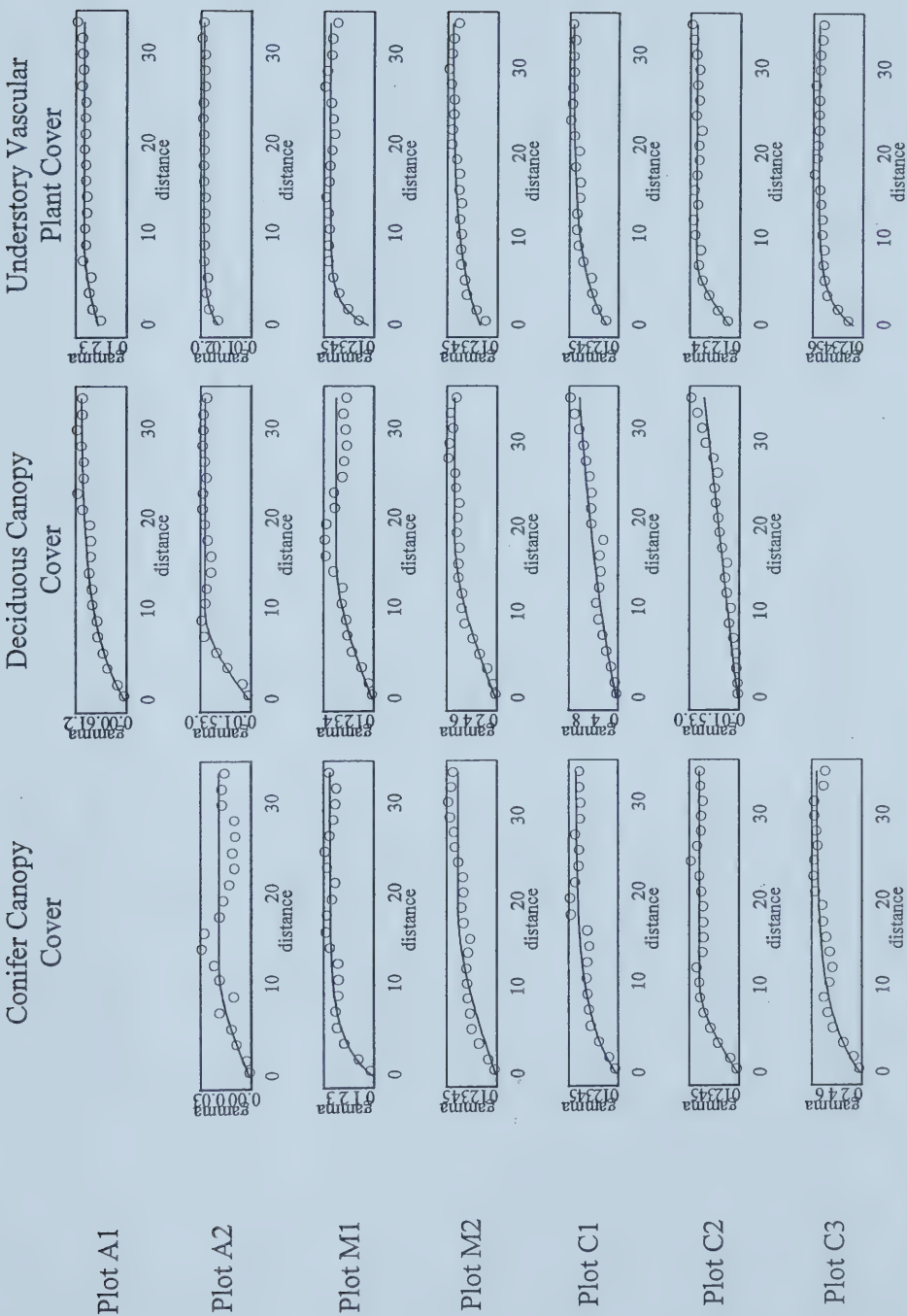
Variables	Stand Type	Proportion of transects in each stand type with negative covariance peaks at a given spatial scale						Proportion of transects in each stand type with positive covariance peaks at a given spatial scale					
		Scale (meters)						Scale (meters)					
		0-2.5	2.5-5	5-7.5	7.5-10	10-12.5	12.5-15	0-2.5	2.5-5	5-7.5	7.5-10	10-12.5	12.5-15
Conifer canopy cover	Aspen												
vs.	Mixed					0.50	0.13					0.13	
Vascular plant cover	Conifer		0.13	0.25		0.33	0.25						
		0.08	0.25	0.08	0.08								
Conifer canopy cover	Aspen												
vs.	Mixed		0.25	0.13		0.25					0.13	0.13	
Non-vascular plant cover	Conifer		0.08	0.42	0.08	0.08	0.08		0.13	0.13	0.08		0.17
		0.08	0.08	0.08	0.08					0.17			
Conifer canopy cover	Aspen												
vs.	Mixed			0.13		0.38	0.13					0.25	
Ordination scores	Conifer			0.08	0.08	0.25	0.25			0.17			0.17
		0.13											
Conifer canopy cover	Aspen												
vs.	Mixed						0.13						
Species richness (S)	Conifer				0.08	0.17							
Conifer canopy cover	Aspen												
vs.	Mixed												
Species diversity (H')	Conifer												
		0.13	0.13		0.13								
Conifer canopy cover	Aspen											0.13	0.38
vs.	Mixed		0.13	0.25	0.13	0.13				0.25	0.13	0.13	
<i>Hylacomium splendens</i> cover	Conifer		0.25	0.08	0.17				0.17		0.17	0.17	0.25
		0.13											
Conifer canopy cover	Aspen											0.13	
vs.	Mixed					0.13	0.13			0.25		0.13	
<i>Linnaea borealis</i> cover	Conifer		0.17	0.08	0.08	0.08	0.08				0.17		
Conifer canopy cover	Aspen												
vs.	Mixed		0.13		0.13	0.13	0.38					0.13	
<i>Rosa acicularis</i> cover	Conifer			0.25		0.08	0.25						





**Figure 3.1.** Quadrat (top) and species (bottom) ordination scores on the first two axes from a DCA ordination of understory vegetation in 3674 quadrats at the EMEND study site. Species abbreviations are listed in Table 3.1.

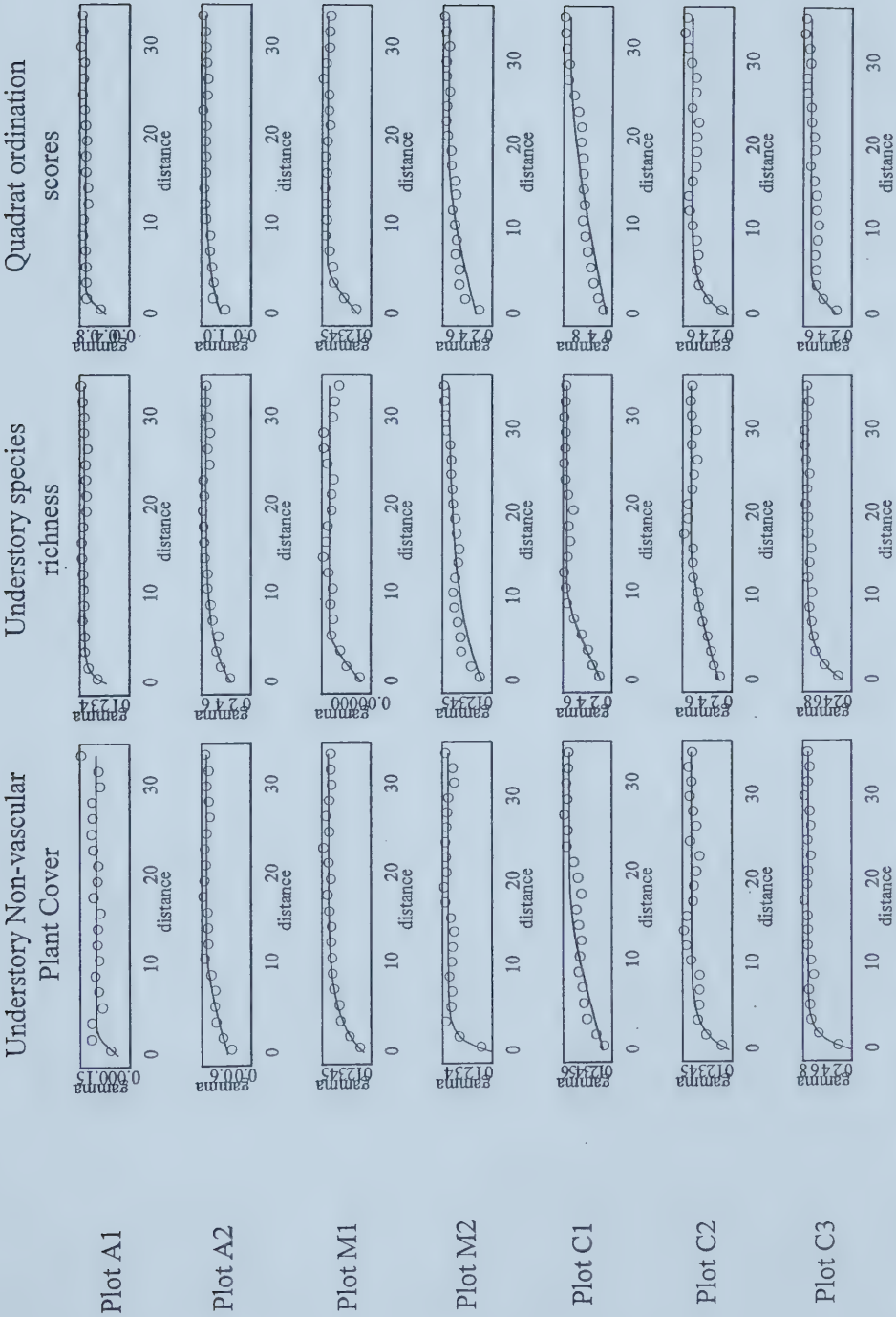




**Figure 3.2.** Empirical semivariogram (gamma) estimates versus distance (in meters) for canopy and understory variables measured in seven study plots at the EMEND study site. The semivariogram model fit to each variable is indicated by the solid line. Semivariogram model type and range of spatial dependence are listed in Table 3.2.

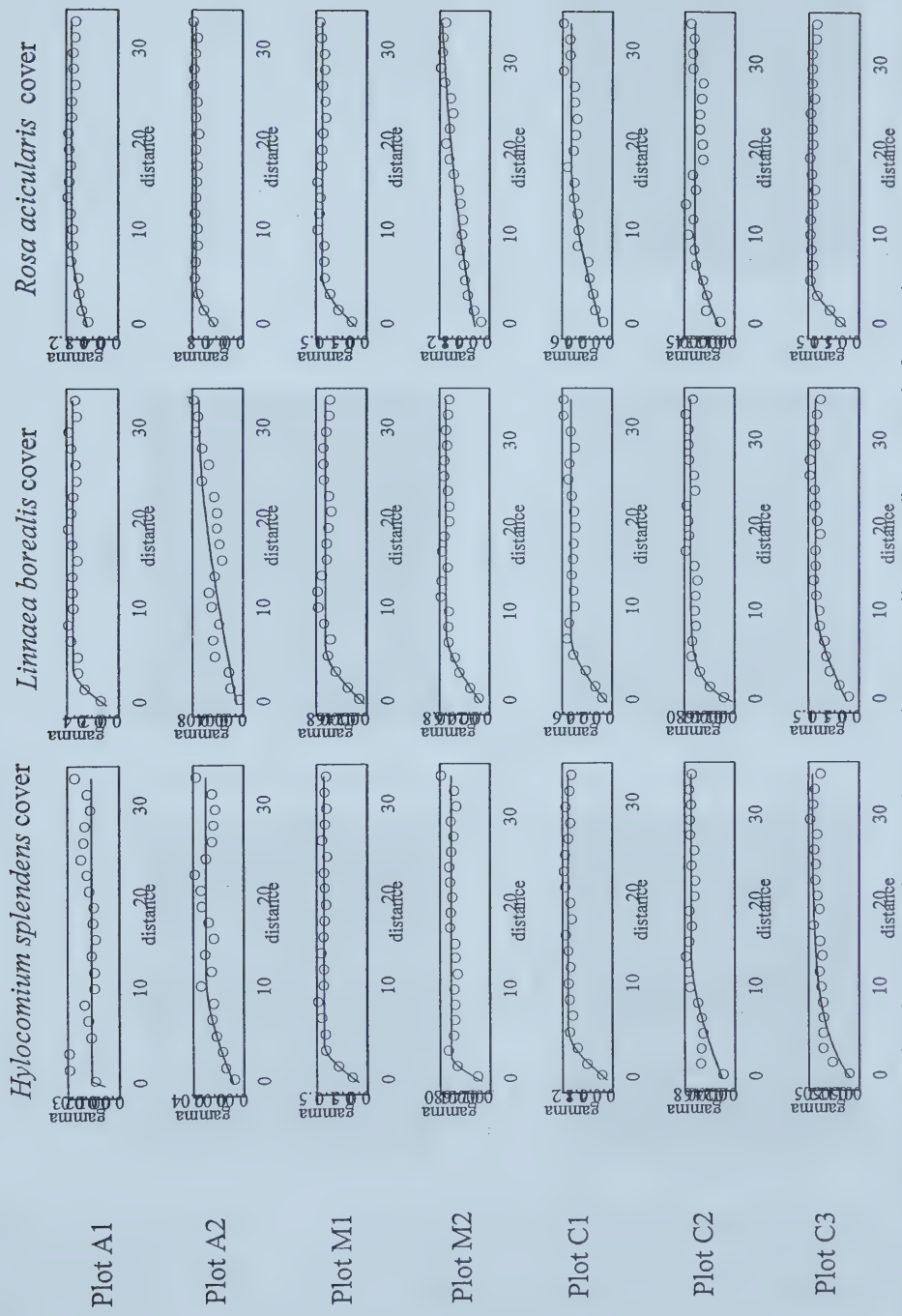






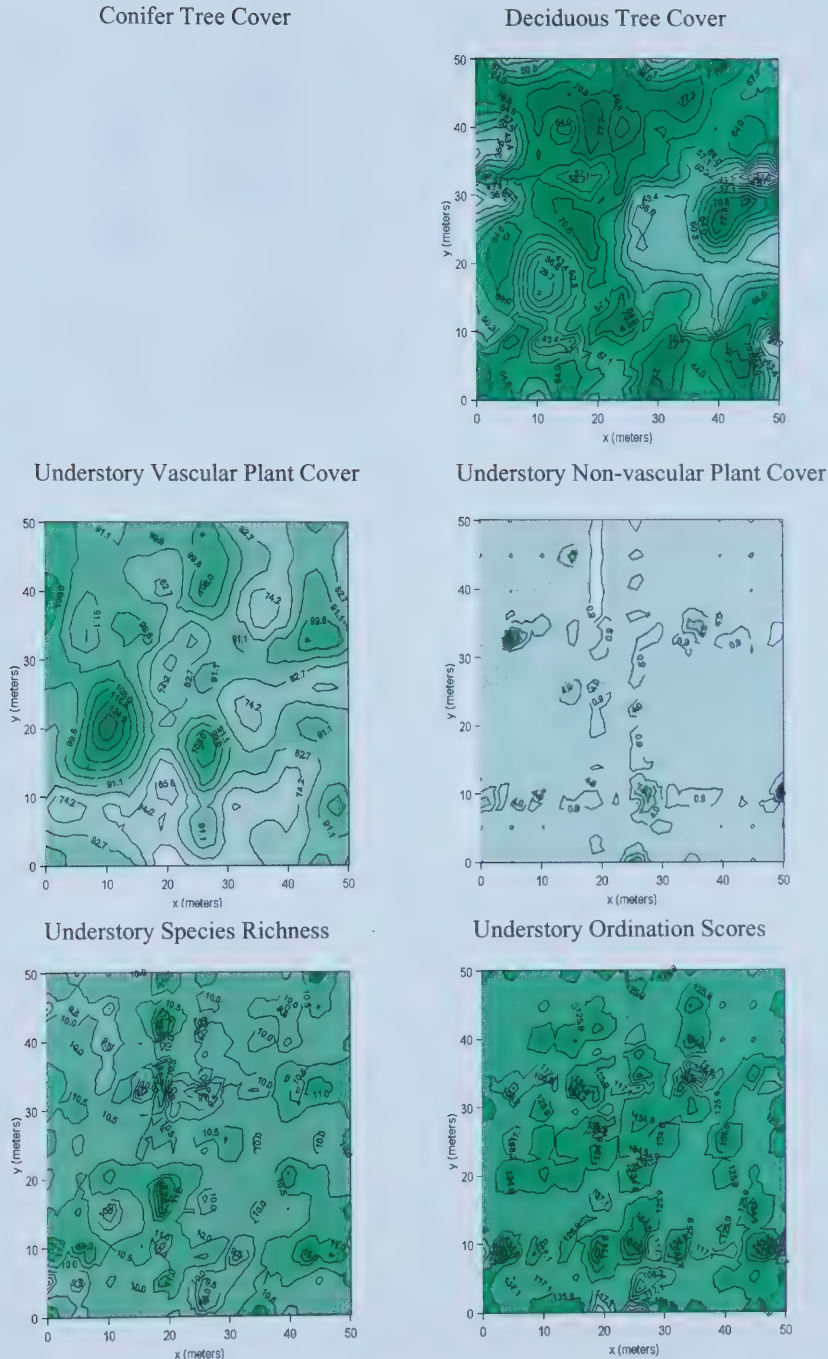
**Figure 3.2 continued.** Empirical semivariogram estimates (gamma) versus distance (in meters) for canopy and understory variables measured in seven study plots at the EMEND study site. The semivariogram model fit to each variable is indicated by the solid line. Semivariogram model type and range of spatial dependence are listed in Table 3.2.





**Figure 3.3.** Empirical semivariogram estimates (gamma) versus distance (in meters) for understory species covers measured in seven study plots at the EMEND study site. The semivariogram model fit to each variable is indicated by the solid line. Semivariogram model type and range of spatial dependence are listed in Table 3.2.

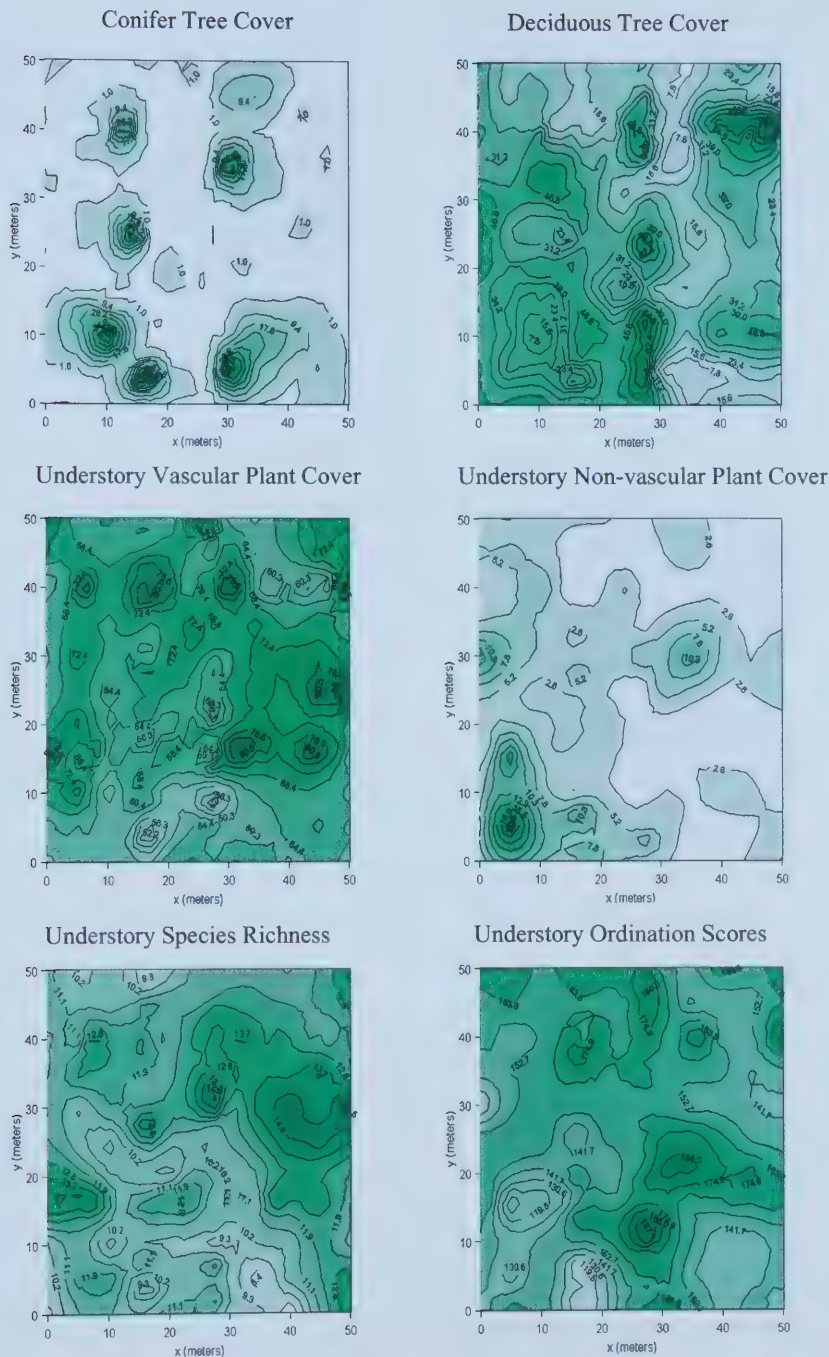




**Figure 3.4.** Maps of Plot A1 based on kriged estimates of values for several canopy and understory variables measured at the EMEND study site. Scale and units vary between maps, with darker colours indicating higher values of the variable. Canopy and understory covers are measured as percent cover, species richness is measured as total number of species, ordination scores are scores of quadrats on the first axis of a DCA ordination of understory vegetation.



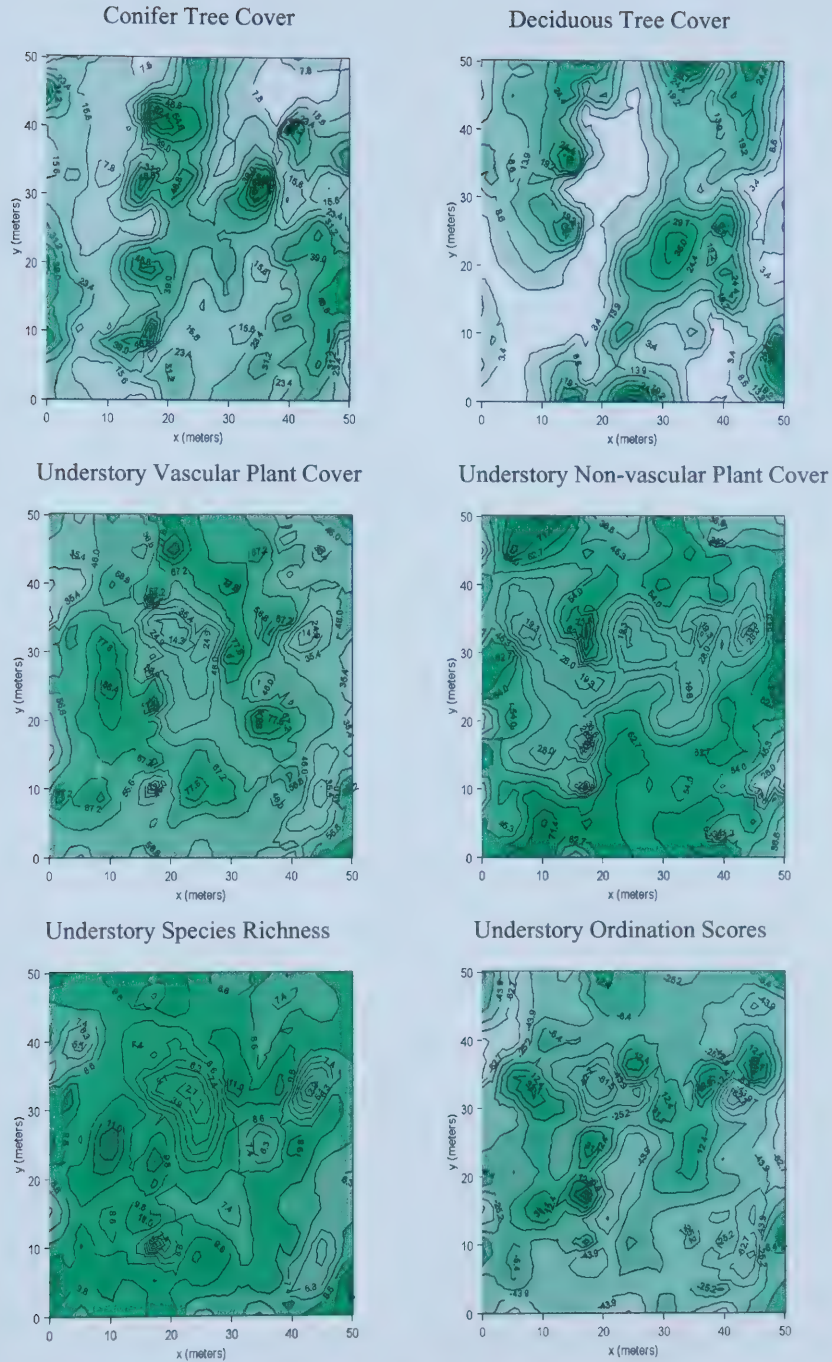




**Figure 3.5.** Maps of Plot A2 based on kriged estimates of values for several canopy and understory variables measured at the EMEND study site. Scale and units vary between maps, with darker colours indicating higher values of the variable. Canopy and understory covers are measured as percent cover, species richness is measured as total number of species, ordination scores are scores of quadrats on the first axis of a DCA ordination of understory vegetation.

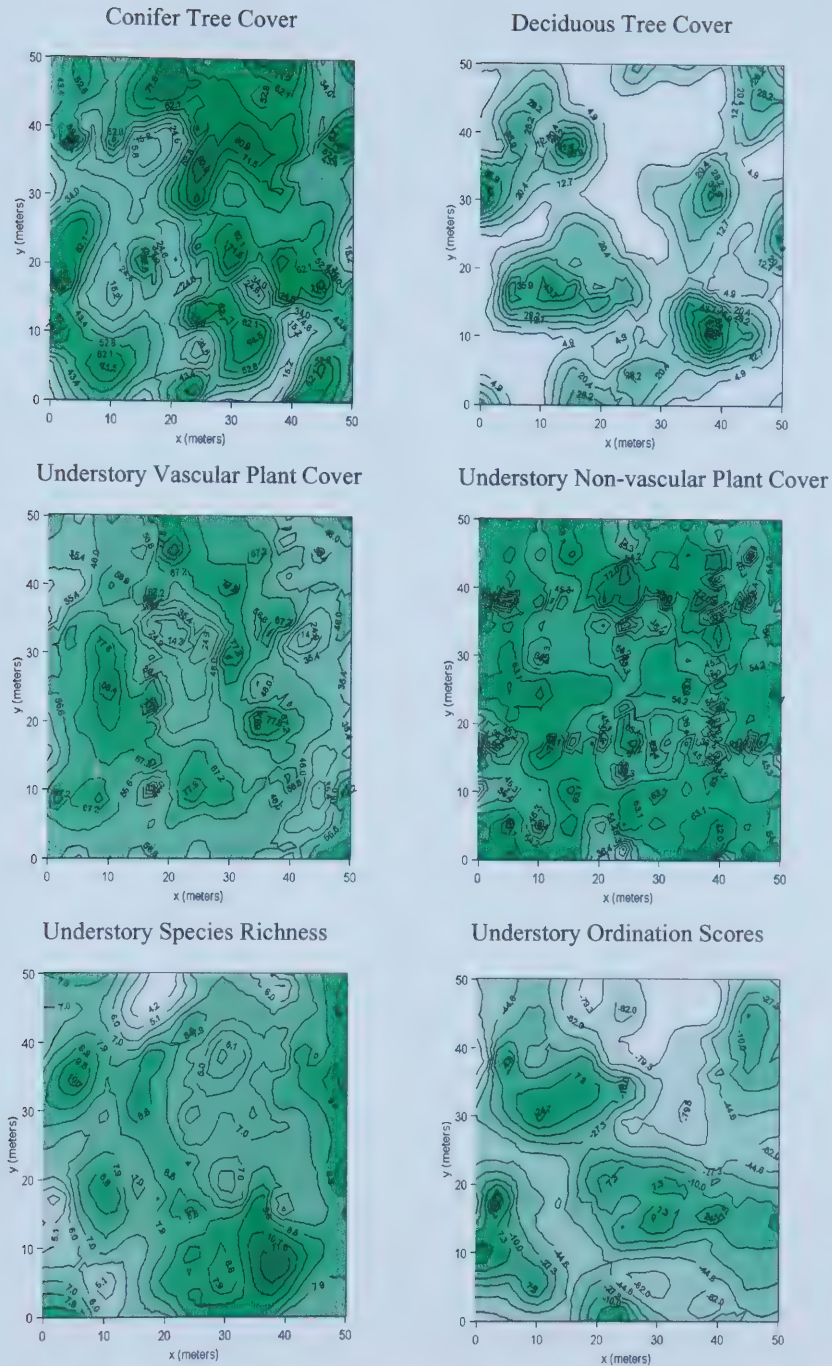






**Figure 3.6.** Maps of Plot M1 based on kriged estimates of values for several canopy and understory variables measured at the EMEND study site. Scale and units vary between maps, with darker colours indicating higher values of the variable. Canopy and understory covers are measured as percent cover, species richness is measured as total number of species, ordination scores are scores of quadrats on the first axis of a DCA ordination of understory vegetation.

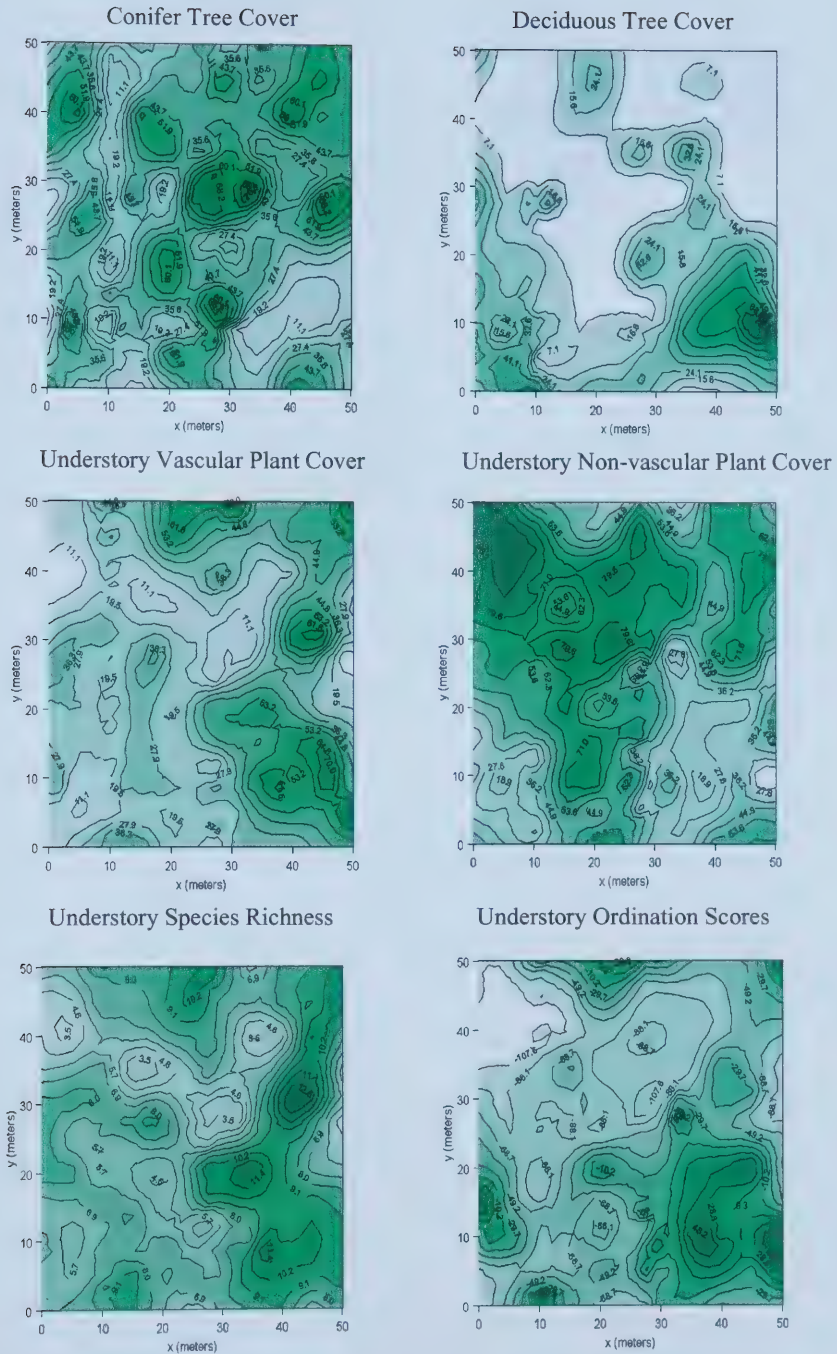




**Figure 3.7.** Maps of Plot M2 based on kriged estimates of values for several canopy and understory variables measured at the EMEND study site. Scale and units vary between maps, with darker colours indicating higher values of the variable. Canopy and understory covers are measured as percent cover, species richness is measured as total number of species, ordination scores are scores of quadrats on the first axis of a DCA ordination of understory vegetation.

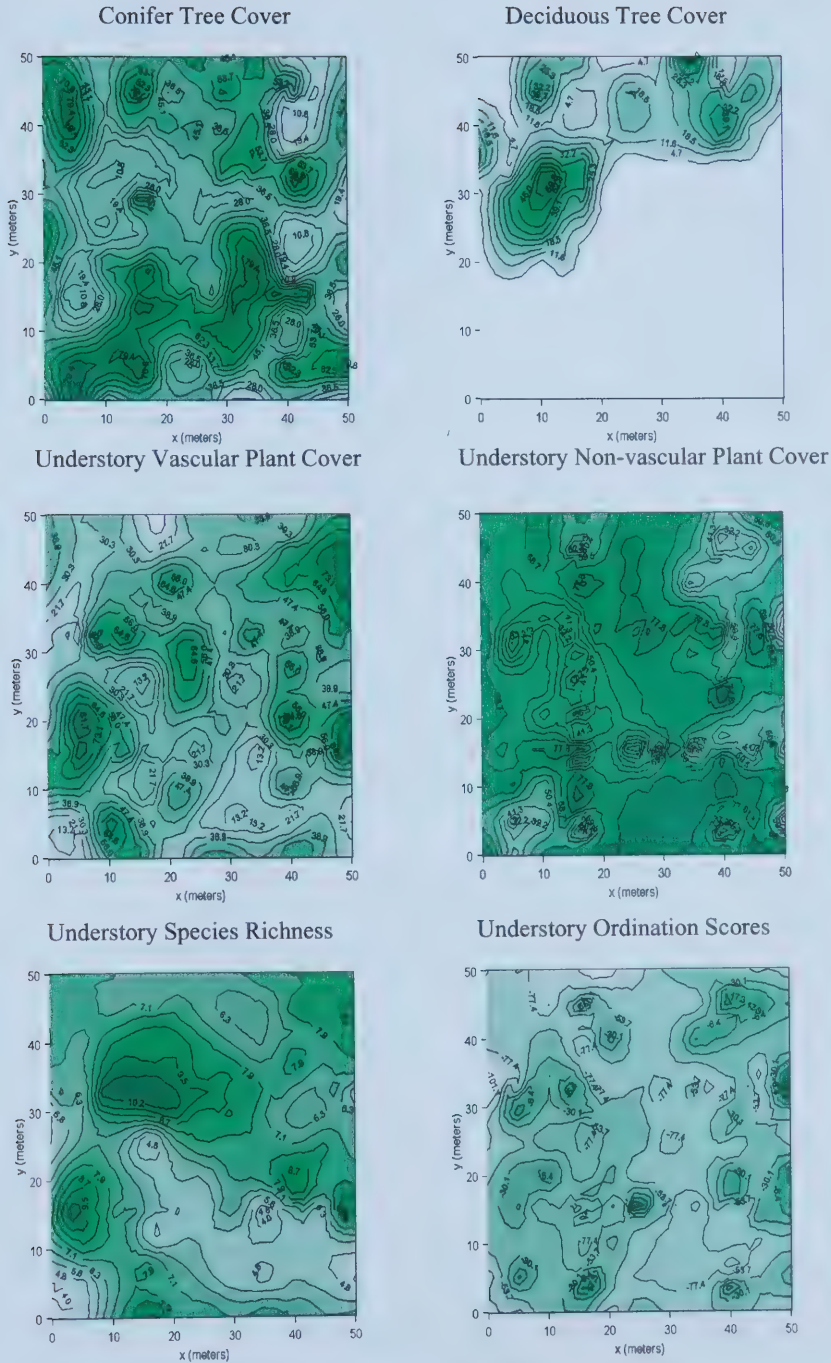






**Figure 3.8.** Maps of Plot C1 based on kriged estimates of values for several canopy and understory variables measured at the EMEND study site. Scale and units vary between maps, with darker colours indicating higher values of the variable. Canopy and understory covers are measured as percent cover, species richness is measured as total number of species, ordination scores are scores of quadrats on the first axis of a DCA ordination of understory vegetation.

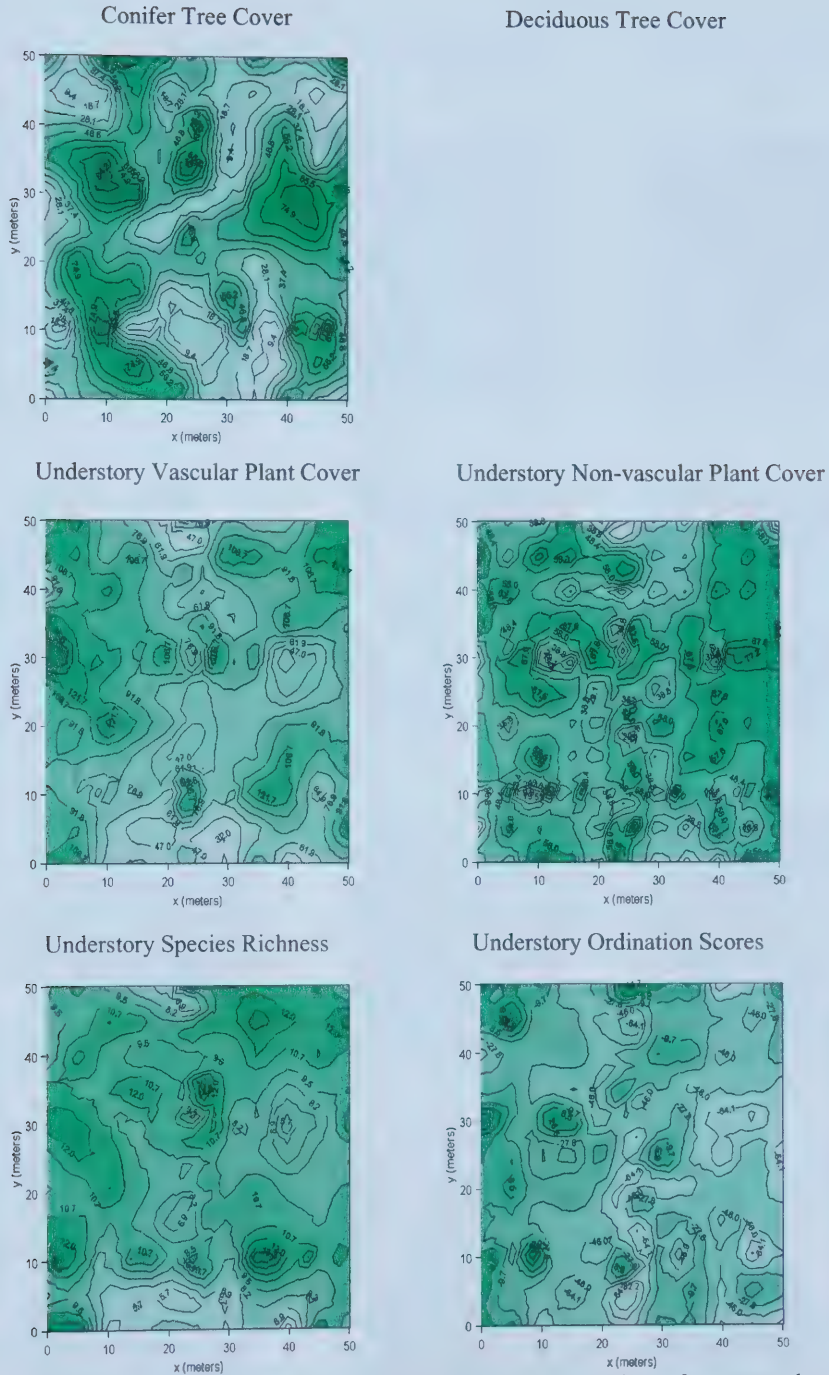




**Figure 3.9.** Maps of Plot C2 based on kriged estimates of values for several canopy and understory variables measured at the EMEND study site. Scale and units vary between maps, with darker colours indicating higher values of the variable. Canopy and understory covers are measured as percent cover, species richness is measured as total number of species, ordination scores are scores of quadrats on the first axis of a DCA ordination of understory vegetation.

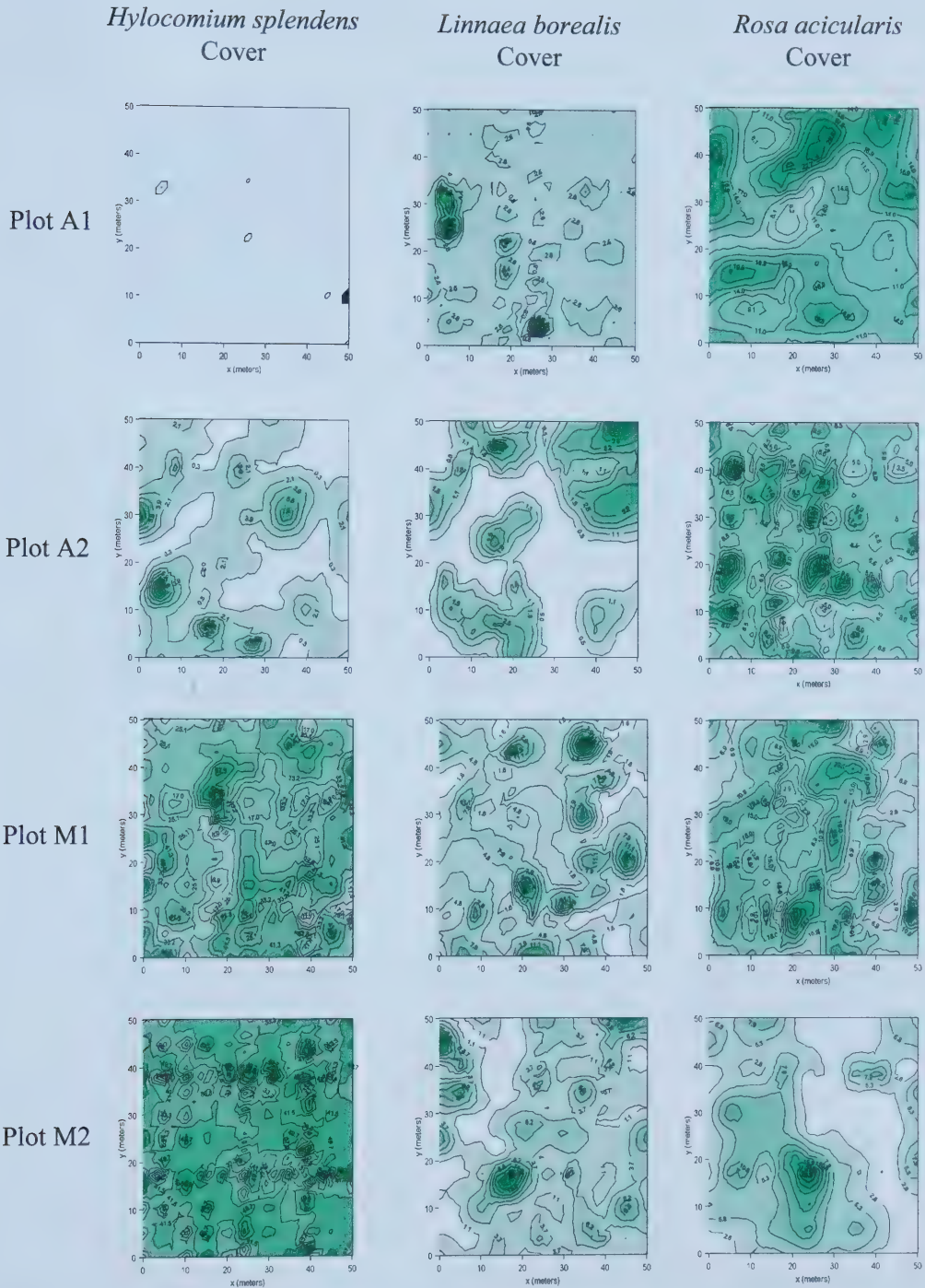






**Figure 3.10.** Maps of Plot C3 based on kriged estimates of values for several canopy and understory variables measured at the EMEND study site. Scale and units vary between maps, with darker colours indicating higher values of the variable. Canopy and understory covers are measured as percent cover, species richness is measured as total number of species, ordination scores are scores of quadrats on the first axis of a DCA ordination of understory vegetation.

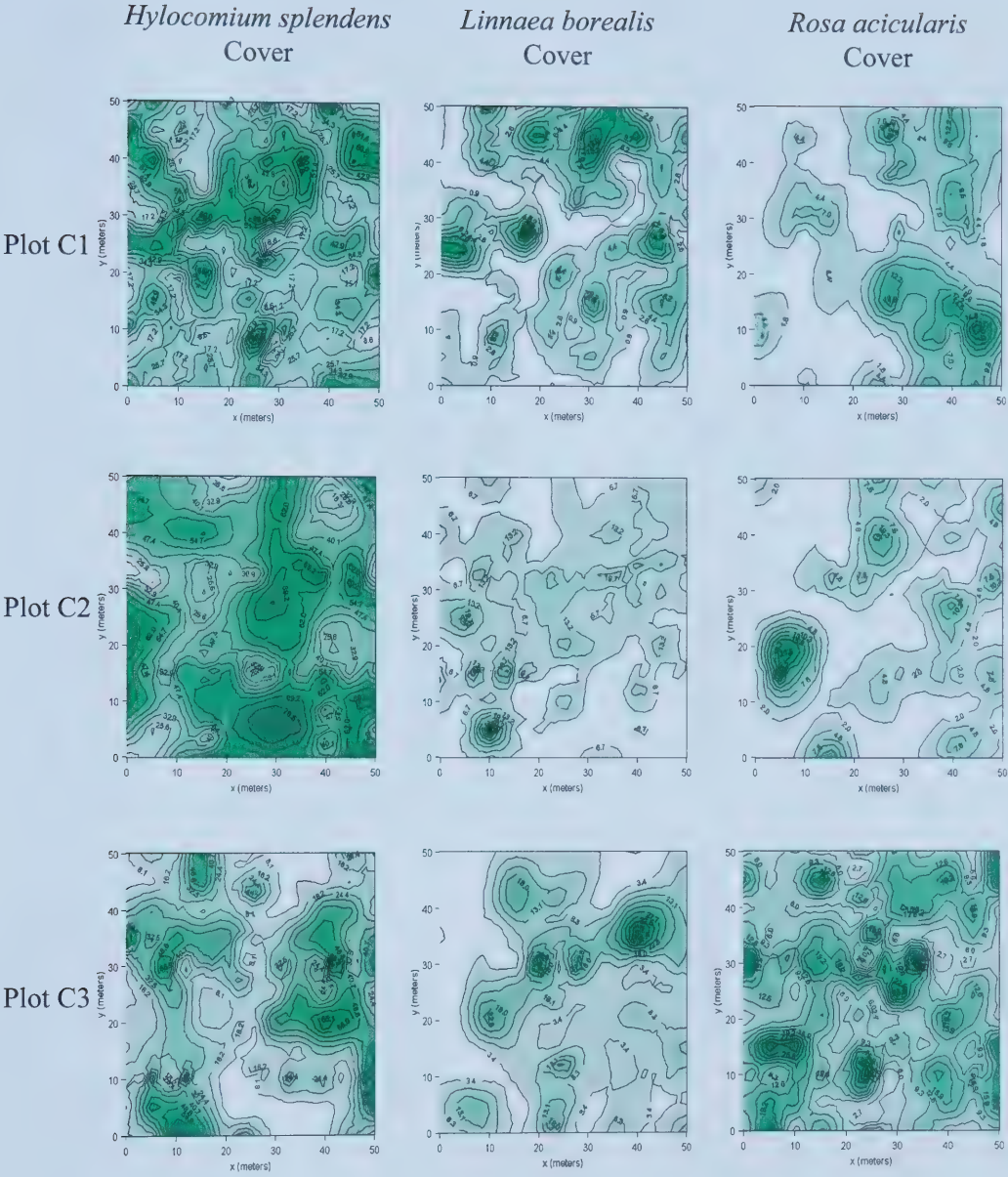




**Figure 3.11.** Maps of all study plots based on kriged estimates of percent cover values for understory species *Hylocomium splendens*, *Linnaea borealis* and *Rosa acicularis*. Scale varies between maps, with darker colours indicating higher values of the variable.

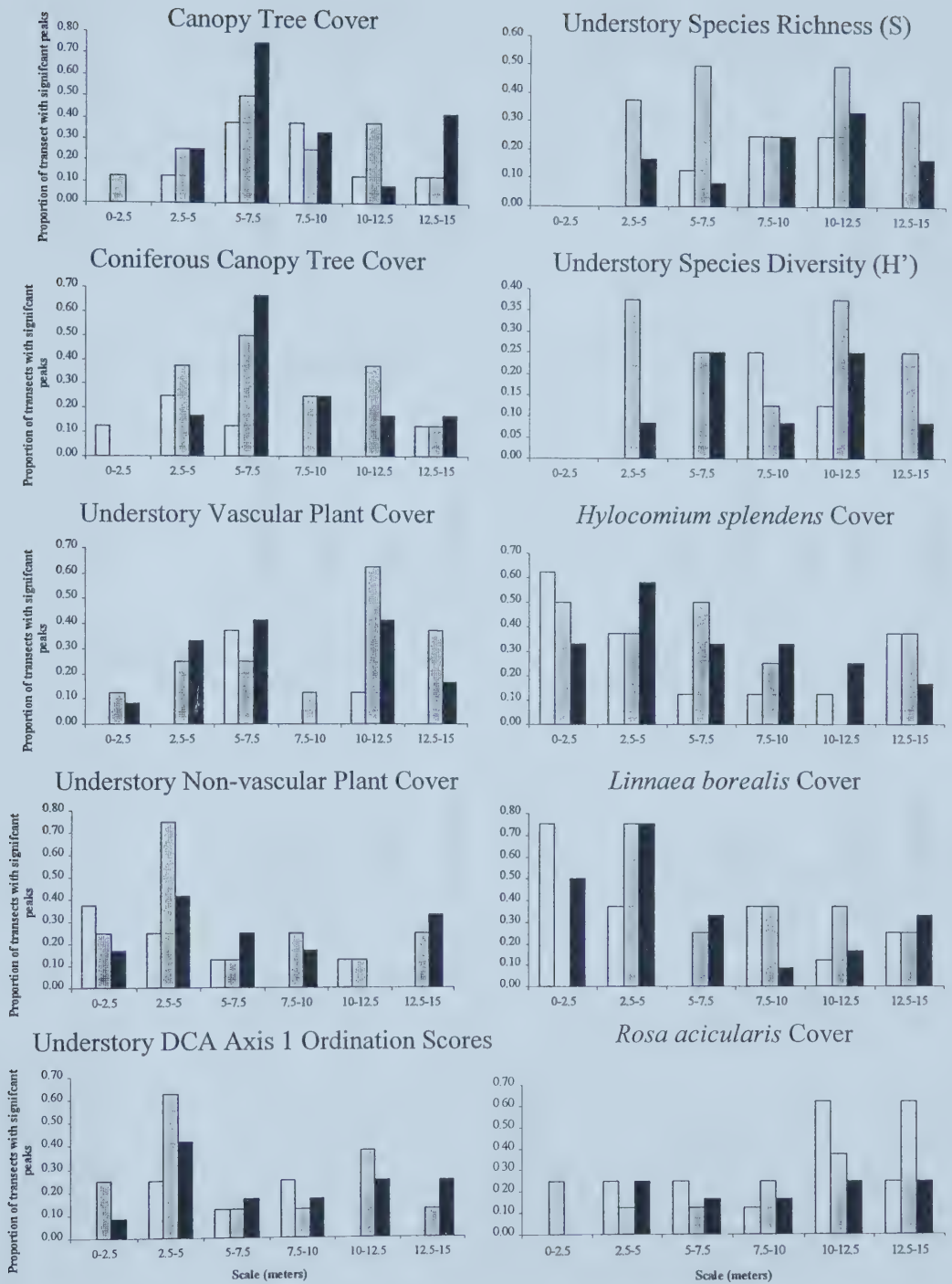






**Figure 3.11 continued.** Maps of all study plots based on kriged estimates of percent cover values for understory species *Hylocomium splendens*, *Linnaea borealis* and *Rosa acicularis*. Scale varies between maps, with darker colours indicating higher values of the variable.

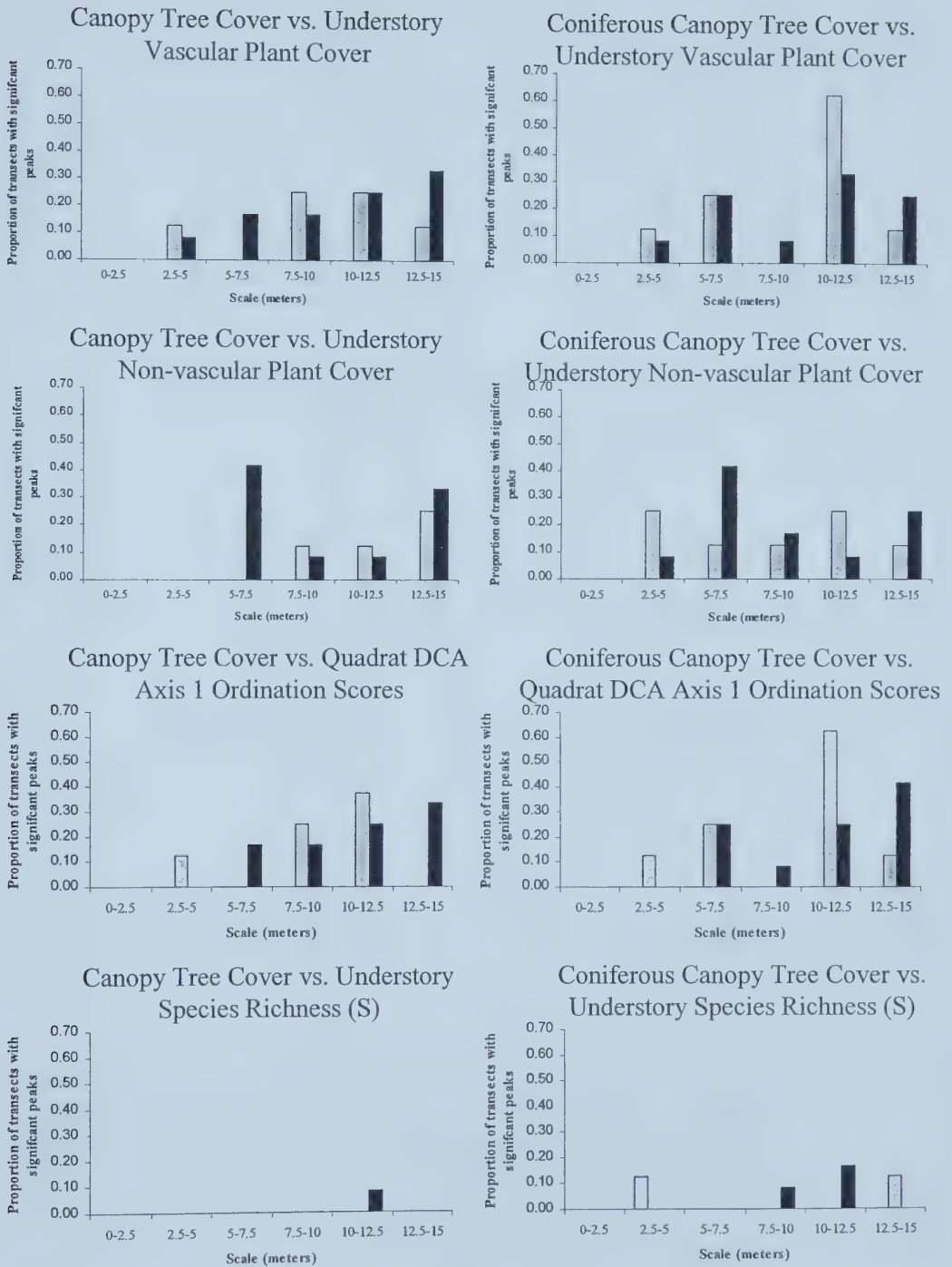




**Figure 3.12.** Summary of proportion of transects with significant variance peaks in each of three plot types (Aspen dominated – white bars, Mixed – gray bars, Conifer dominated – black bars) versus spatial scale for canopy and understory variables in study plots at the EMEND study site.

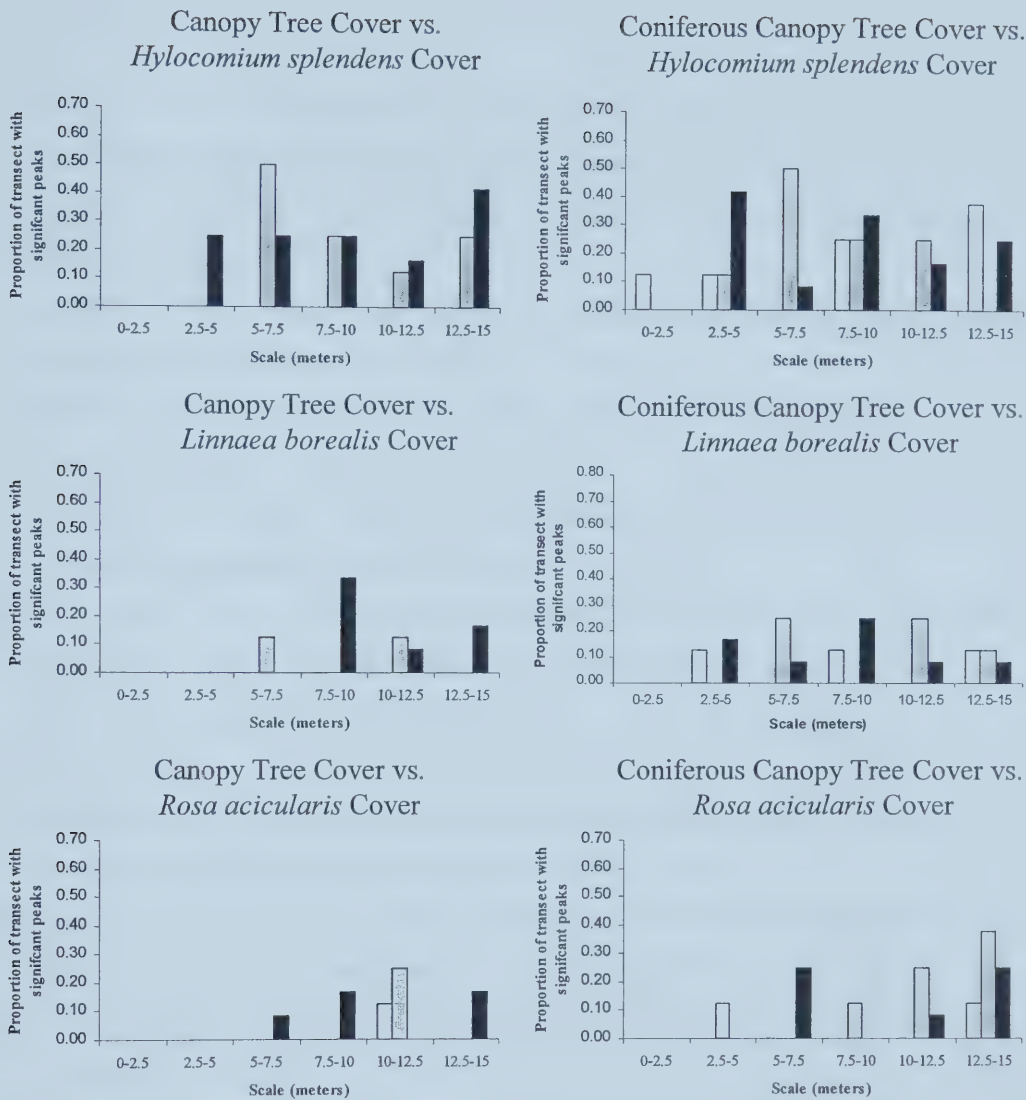






**Figure 3.13.** Summary of proportion of transects with significant covariance peaks in each of three plot types (Aspen dominated – white bars, Mixed – gray bars, Conifer dominated – black bars) versus spatial scale for canopy and understory variables in study plots at the EMEND study site.





**Figure 3.13 continued.** Summary of proportion of transects with significant covariance peaks in each of three plot types (Aspen dominated – white bars, Mixed – gray bars, Conifer dominated – black bars) versus spatial scale for canopy and understory variables in study plots at the EMEND study site.



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## CHAPTER 4

### GENERAL CONCLUSIONS AND FUTURE RESEARCH

#### Conclusions

In this thesis, I studied the spatial patterns of boreal mixedwood vegetation at small spatial scales. Spatial analyses of tree populations, and of relationships between canopy and understory vegetation, indicated the usefulness of a multiscale approach to ecological research. Many of the patterns I observed in canopy and understory vegetation were only found at certain scales of analysis, and in some cases the nature and strength of ecological patterns and relationships changed with the scale of observation.

With regards to the objectives listed in Chapter 1, my findings were that the spatial patterns of boreal mixedwood tree populations, canopy cover and understory communities were all very patchy at small spatial scales. Canopy structure appeared to play an important role in determining distribution patterns of understory tree and non-tree vegetation at a range of small spatial scales. Canopy conifers showed a stronger influence on the distribution of understory plants than canopy deciduous trees, and the overall influence of the canopy on understory trees and the understory plant community increased along a gradient of increasing conifer presence in the canopy.

Canopy gaps were important regeneration sites for understory trees, and the cover of many understory vascular species was highest under canopy gaps. The density of white spruce seedlings was higher under canopy gaps than under closed canopy areas, especially in Mixed and Conifer dominated stands. Understory aspen trees did not show as strong of a response to canopy structure as white spruce did, possibly due to the small size of canopy gaps in the study plots not providing sufficient light and temperature increases to trigger aspen suckering in gaps. Understory vascular plant covers were often higher under gaps in Mixed and Conifer forests, but not in Aspen stands, while non-vascular plants were often found growing under conifer tree patches in all stand types. In general, Mixed and Conifer dominated stand understories were more heterogenous in their community composition and distributions of tree regeneration, possibly due to the



ability of canopy conifer trees to create a more heterogeneous light and soil environment in the understory.

## **Future research**

This study was able to document patterns of structure and relationships between canopy and understory vegetation in boreal mixedwood forests, but did not address the specific mechanisms that gave rise to observed patterns. Further research which focuses on the relationships between canopy structure and patterns of understory resource availability and environmental heterogeneity, mechanisms of canopy effects on the distribution of understory tree and non-tree species, and the influence of other factors such as dispersal limitation, competition and herbivory on the distribution of understory species, will be needed to determine which ecological processes are responsible for structuring understory communities and patterns of tree regeneration at small spatial scales. Direct manipulations of canopy structure and monitoring of understory response to changes in canopy structure at a range of spatial scales would be an excellent way to approach these questions experimentally.

The increasing availability of, and interest in, spatial analysis tools for ecological data has allowed many advances in ecological research which were not previously possible (Dale 1999). Many of these tools are still in need of further development, and much work remains to be done in creating and applying new methods. The wavelet randomization method used in Chapter 3 was a new technique developed for this study which will require further testing and improvement, especially with regards to its ability to deal with spatially autocorrelated data, but which may prove useful in other studies where researchers wish to examine multiscale patterns and relationships, and test their statistical significance.

A central theme of this thesis is that the processes that are important in structuring plant communities may vary depending on the spatial and temporal scale of observation. At small spatial scales, canopy structure plays an important role in determining patterns of understory vegetation, but other factors such as competition, herbivory, soil type, moisture regime, site history and biogeographic processes are also important at a range of



spatial scales (Collins et al. 1985, Tonteri 1994, Dlott and Turkington 2000, Ehrlen and Eriksson 2000). It would be extremely useful to link this study of the small-scale spatial patterns of boreal forest vegetation to studies at larger spatial and temporal scales (e.g. Qian et al. 1998, Brosofske et al. 1999) to determine how processes operating at a larger range of scales create the patterns of biodiversity which were observed in boreal mixedwood forests in Alberta. It would also be useful to continue monitoring the spatial structure of boreal vegetation over longer time periods to determine how canopy and understory structure and relationships vary temporally as well as spatially. A better understanding of the patterns and processes which maintain biological diversity at all spatial scales is a central goal of ecology (Levin 1992), and hopefully this study has contributed to our understanding of some of these patterns.

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